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Interactions between non-native oysters (*Crassostrea gigas* Thunberg) and native eelgrass (*Zostera marina* L.) and consequences for intertidal community structure in the Strait of Georgia, British Columbia, Canada

by

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ABSTRACT

Effects of the introduced Pacific oyster (*Crassostrea gigas*) on native eelgrass (*Zostera marina*) health and intertidal community structure were investigated on Cortes Island, British Columbia, Canada. While oysters and eelgrass coexist regionally, eelgrass is typically absent directly seaward of oysters on Cortes Island. Nektonic and epibenthic assemblages were compared between eelgrass and below-oyster habitats (BOH) to assess impacts of shifting from eelgrass to BOH. Epibenthic species richness and abundance were higher in BOH than in eelgrass beds, while nektonic species richness and abundance were higher in eelgrass beds than in BOH. An eelgrass transplant experiment was conducted to determine suitability of the below-oyster zone for eelgrass growth. Shoot and leaf number were significantly greater over time in eelgrass bed transplants than in below-oyster transplants. These results suggest that further expansion of oyster beds will result in increased eelgrass loss and a dramatic shift in intertidal community structure.

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TABLE OF CONTENTS

1. **Introduction** 1
   References 7

2. **Indirect effects of non-native oyster (Crassostrea gigas Thunberg) on native eelgrass (Zostera marina L.) in the Strait of Georgia** 12
   Introduction 12
   Methods 15
      Study sites 15
      Eelgrass transplants 16
      Oyster transplants 16
      Statistical methods 17
   Results 18
      Eelgrass transplants 18
      Oyster transplants 19
   Discussion 19
   References 33

3. **Displacement of native eelgrass (*Zostera marina* L.) by introduced oysters (*Crassostrea gigas* Thunberg) significantly alters intertidal community structure** 38
   Introduction 38
   Methods 40
      Study sites 40
      Epibenthic macroinvertebrates and macroalgae 41
      Fish and swimming macroinvertebrates 42
      Statistical methods 42
   Results 43
      Epibenthic macroinvertebrates and macroalgae 43
      Fish and swimming macroinvertebrates 44
   Discussion 45
   References 58

4. **Conclusions** 62
   References 67

Appendix 70

LIST OF TABLES

Table 2-1. Results of repeated measures ANOVA for each eelgrass transplant site.. 25

Table 2-2. Relative abundance of green alga *Enteromorpha intestinalis* at eelgrass transplant sites.....26

Table 3-1. Epibenthic macrinvertebrate and macroalgae species richness in eelgrass and below-oyster transects.....49

Table 3-2. Percent cover of plants and epibenthic macroalgae in eelgrass and below-oyster transects 49

Table 3-3. Most abundant macroinvertebrate taxa in eelgrass and below-oyster transects 50

Table 3-4. Fish and swimming macroinvertebrate species richness in eelgrass and below-oyster seine hauls.....50

Table 3-5. Most abundant fish and swimming macroinvertebrate species in eelgrass and below-oyster seine hauls.....51

LIST OF FIGURES

Figure 2-1. Map of Cortes Island with detail of study site locations 27

Figure 2-2. Study site layout 28

Figure 2-3. Schematic diagram of eelgrass transplant experiment 28

Figure 2-4. Schematic diagram of oyster transplant experiment 29

Figure 2-5. Change in average number of eelgrass shoots per transplant over time in eelgrass and below-oyster zone 30

Figure 2-6. Change in average number of leaves per transplant over time in eelgrass and below-oyster zone 31

Figure 2-7. Sediment sulphide concentraions 32

Figure 3-1. Map of Cortes Island with detail of study sites 52

Figure 3-2. Study site layout 53

Figure 3-3. Two-dimensional ordination of transect data 54

Figure 3-4. Dendrogram of fish and swimming macroinvertebrate assemblages in eelgrass and below-oyster habitats 55

Figure 3-5. Fish and swimming macroinvertebrates caught in seines at eelgrass bed and below-oyster sites 56

Figure 3-6. Examples of below-oyster habitat and eelgrass bed habitat 57

Figure 4-1. Schematic diagram of eelgrass-oyster interactions on Cortes Island based on literature and thesis research results 66

INTRODUCTION

Human-mediated introductions of non-native species have occurred in marine habitats worldwide; some introductions have been accidental, such as larvae transported in ballast water, while others have been intentional for aquaculture or fishery purposes (Carlton and Geller 1993, Carlton 1996, Ruiz *et al.* 1999, Grosholz *et al.* 2000, Crooks 2001, Waknitz *et al.* 2003, Rudnick *et al.* 2005). Many introduced species are detrimental to native species through predation, competition, or habitat modification (Carlton and Geller 1993, Carlton 1996, Reusch and Williams 1998, Grosholz *et al.* 2000, Crooks 2001, Branch and Steffani 2004, Ross *et al.* 2004). The effects of a non-native species on the invaded environment may be particularly dramatic if it harms a native organism that provides habitat for other native species (Crooks 2002, Lodge 1993).

Organisms that play a significant role in creating, maintaining or modifying habitat have called ecosystem engineers (Jones *et al.* 1994, 1997, Coleman and Williams 2002). Important marine ecosystem engineers include mangroves, reef-forming corals, and seagrasses (Coleman and Williams 2002, Loreto *et al.* 2003, Mumby *et al.* 2004). Many successful marine invaders also act as ecosystem engineers in their new environments (Crooks 2002, Lodge 1993). For example, a macroalga native to the Phillipines, *Gracilaria salicornia* (Agardh), dominates benthic habitats in Waikiki, Hawaii, where its mat-forming habit allows it to monopolize nutrients and exclude native macroalgae (Smith *et al.* 2004). An invasive alga off the coast of France, *Caulerpa taxifolia* (Vahl), has outcompeted native seagrasses and covers the substratum with a dense rhizoidal mat that prevents foraging by native fish (Levi and Francour 2004). The Asian date mussel, *Musculista senhousia* (Benson), has invaded regions as disparate as

the Adriatic Sea and San Diego Bay, California (Reusch and Williams 1998, Mistri 2003). In addition to outcompeting native suspension-feeding invertebrates, *M. senhousia* forms extensive mats with its byssal threads, preventing native deposit-feeders from foraging in the sediment.

San Francisco Bay, California, is a classic example of a heavily-invaded ecosystem due to heavy shipping traffic carrying ballast water, stocking of non-native fish and molluscs, escapes from aquaculture facilities, and high levels of natural and human disturbance that facilitate biological invasions (Cohen and Carlton 1998, Grosholz *et al.* 2000, Rudnick *et al.* 2005). Ballast-water- and aquaculture-mediated introductions are an issue of increasing importance in other areas along the west coast of North America (Naylor *et al.* 2003, Waknitz *et al.* 2003, Rudnick *et al.* 2005). In British Columbia, Canada, farmed non-indigenous species include Atlantic salmon (*Salmo salar* L.), the Manila clam (*Venerupis philippinarum* Adams and Reeve), and the Pacific oyster (*Crassostrea gigas* Thunberg) (BCSGA 2003, Naylor *et al.* 2003, Brooks *et al.* 2004, Kruzynski 2004).

The Pacific oyster was introduced to British Columbia from Japan in the 1920s, and the first major spawning of these oysters was recorded in 1932 (Quayle 1964). Spawning of cultured oysters resulted in the establishment of feral populations on most islands in the Strait of Georgia by 1958 and many populations continue to spawn annually in late summer (Quayle 1964, 1988). The shellfish aquaculture industry in British Columbia plans to more than triple shellfish production from its 2002 wholesale value of $20 million by 2007, with a projected $30 million increase in oyster and clam production (BCSGA 2003, Wilson 2003).

Along with several natural and anthropogenic factors, expansion of feral and cultured oyster beds may threaten native eelgrass in British Columbia and the Pacific Northwest of the United States (Short and Wyllie-Echeverria 1996, Wright 2002, Wyllie-Echeverria *et al.* 2003). Significant eelgrass losses have been noted in coastal British Columbia, Washington and Oregon (Griffin 1997, Wright 2002, Wyllie-Echeverria *et al.* 2003). Dredging and filling for harbour construction, shading by docks, sedimentation due to logging, introduction of toxic chemicals in runoff, increased nutrient input from septic systems, bioturbation by burrowing invertebrates and grazing pressure from Canada geese (*Branta canadensis* L.) have been cited as factors contributing to eelgrass loss in these areas (Wright 2002, Wyllie-Echeverria *et al.* 2003). Few studies have dealt with the possible role of oyster-eelgrass interactions in eelgrass loss in British Columbia and the Pacific Northwest of the United States (Waddell 1964).

Oysters and eelgrass are both found in relatively wave-sheltered areas, with oysters occupying the mid-to-high intertidal zone and eelgrass occupying the low intertidal to shallow subtidal zone (Dumbauld and Wyllie-Echeverria 2003, pers. obs.). Although eelgrass and oyster beds can be found in close proximity, eelgrass is typically absent directly seaward from oyster beds (Everett *et al.* 1995, pers. obs.). Oyster presence has also been correlated with decreased eelgrass abundance (Waddell 1964, Everett *et al.* 1995). Eelgrass serves as an ecosystem engineer in native habitats along the British Columbia coast by providing refuge from predation and slowing ocean currents, and supports a diverse array of fish and invertebrates including juvenile salmonids (*Oncorhynchus* spp.), Pacific herring (*Clupea harengus* L.), and Dungeness crab (*Cancer magister* Dana) (Marsh 1973, Heck and Orth 1980, Lubbers *et al.* 1990,

Jones *et al.* 1994, Griffin 1997, Murphy *et al.* 2000, Coleman and Williams 2002, Wyllie-Echeverria *et al.* 2003). Therefore, eelgrass loss would likely be detrimental to many species and could result in a dramatic shift in intertidal community composition. Quantifying differences in community structure between eelgrass beds and eelgrass-free habitat seaward of oysters is a critical first step toward understanding the impacts of eelgrass loss.

The Pacific oyster may also act as an ecosystem engineer by altering water flow due to its physical structure and high filtration rate, increasing habitat complexity in the high-intertidal zone due to its physical structure, adding large quantities of organic matter to the sediment, and possibly by causing sulphide accumulation in the sediment (Castel *et al.* 1989). Oyster beds support abundant macrofauna including small gastropods that use oyster shells as a hard substratum for attachment, and shore crabs that forage on small gastropods and use oyster shells for shelter (Griffin 1997). Although separate studies of eelgrass and oyster assemblages exist (Orth *et al.* 1984, Phillips 1984, Fukao 1995, Nugues 1996, Murphy *et al.* 2000), comparisons of eelgrass assemblages to those on or adjacent to oyster beds are rare (eg. Castel *et al.* 1989, Trianni 1996).

Sulphide accumulation in the sediment seaward of oyster beds may play a role in the apparent exclusion of eelgrass by oysters. The large quantity of organic matter added to the sediment by oysters in the form of feces and pseudofeces is associated with hypoxic sediment conditions, which promote the growth of sulphate-reducing bacteria (Ingold and Havill 1984, Castel *et al.* 1989, Nugues 1996, Sorokin *et al.* 1999, deZwaan and Babarro 2001, Kaiser 2001). These bacteria release sulphide, which is associated with reduced photosynthesis and growth in eelgrass (Goodman *et al.* 1995, Holmer and

Bondgaard 2001). Transplants have been used around the world to combat seagrass loss, but success of seagrass restoration depends on the cause of loss as well as the degree of environmental change following seagrass loss (Homziak *et al.* 1982, Harrison 1987, 1990, deJonge *et al.* 1996, Reusch and Williams 1998, Peralta *et al.* 2003). Few experiments testing the ability of eelgrass to survive near oysters have been published (eg. Waddell 1964).

The overall objective of my study was to investigate the impacts of oysters on native eelgrass health and to assess the consequences of eelgrass loss on intertidal community structure. I studied eelgrass beds and nearby oyster beds on the southwest coast of Cortes Island, British Columbia (50°4′N, 124°56′W). Cortes Island is among the most productive areas for shellfish aquaculture in British Columbia (BCSGA 2003, Truscott *et al.* 2005).

Oysters are cultured on Cortes Island using one of two methods: off-bottom raft culture or beach culture (BCSGA 2003). In the off-bottom culture method, oysters are placed on large trays that are suspended from rafts or long lines in deep water (Quayle 1964, 1988, BCSGA 2003). In the beach culture method, oysters are grown directly on the sediment in the intertidal zone (Quayle 1964, 1988, BCSGA 2003). Abundant feral oyster beds are also present on the island, their structure closely approximating that of beach-culture beds (pers. obs.). Beach-culture tenures for oyster and clam aquaculture currently occupy approximately 48 ha on Cortes Island, while off-bottom culture occupies approximately 21 ha (Truscott *et al.* 2005). All eight provincial planning units on and around Cortes Island are considered acceptable or conditionally acceptable for further development of beach culture; eelgrass beds have been identified in seven of eight

planning units (Truscott *et al.* 2005). Ecological effects of oyster beds on native community structure must be investigated in order to predict and mitigate impacts of these proposed increases in farmed populations.

STUDY OBJECTIVES

I had two main objectives:

1) to test the hypothesis that high sulphide levels below Pacific oyster beds are the result of oyster presence, and that conditions below oyster beds are inhospitable to recolonisation by eelgrass.
2) to compare the assemblages of fish and swimming macroinvertebrates, and of epibenthic macroinvertebrates and macroalgae, between eelgrass beds and below-oyster habitats without eelgrass in order to assess the impact on intertidal community structure of replacing eelgrass beds with below-oyster zones.

REFERENCES

BCSGA. 2003. Information resource centre. BC Shellfish Growers Association http://www.bcsga.ca. Accessed 21 Feb 2005.

Branch, G. M., and C. N. Steffani. 2004. Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). Journal of Experimental Marine Biology and Ecology **300**:189-215.

Brooks, K. M., A.R. Stierns, and C. Backman. 2004. Seven year remediation study at the Carrie Bay Atlantic salmon (*Salmo salar*) farm in the Broughton Archipelago, British Columbia, Canada. Aquaculture **239**:81-123.

Carlton, J. T. 1996. Pattern, process and prediction in marine invasion ecology. Biological Conservation **78**:97-106.

Carlton, J. T., and J.B. Geller. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. Science **261**:78-82.

Castel, J., J-P. Labourg, V. Escaravage, I. Auby, and M.E. Garcia. 1989. Influence of seagreass beds and oyster parks on the abundance and biomass patterns of meio- and macrobenthos in tidal flats. Estuarine, Coastal and Shelf Science **28**:71-85.

Cohen, A. N., and J.T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science **279**:555-558.

Coleman, F. C., and S.L Williams. 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends in Ecology and Evolution **17**:40-44.

Crooks, J. A. 2001. Assessing invader roles within changing ecosystems: historical and environmental perspectives on an exotic mussel in an urbanized lagoon. Biological Invasions **3**:23-26.

Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos **97**:153-166.

deJonge, V. N., deJong, D.J., and van den Bergs, J. 1996. Reintroduction of eelgrass (*Zostera marina*) in the Dutch Wadden Sea; review of research and suggestions for management measures. Journal of Coastal Conservation **2**:149-158.

deZwaan, A., and J.M.F. Babarro. 2001. Studies on the causes of mortality of the estuarine bivalve *Macoma balthica* under conditions of (near) anoxia. Marine Biology **138**:1021-1028.

Dumbauld, B. R., and S. Wyllie-Echeverria. 2003. The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. Aquatic Botany **77**:27-42.

Everett, R., G.M. Ruiz, and J.T. Carlton. 1995. Effect of oyster mariculture on submerged aquatic vegetation - an experimental test in a Pacific Northwest estuary. Marine Ecology Progress Series **125**:205-217.

Fukao, R. 1995. The summer invertebrate fauna in and around the eelgrass beds in Koajiro Bay and Moroiso Bay, Miura Peninsula, Central Japan. Physiology and Ecology Japan **31**:21-38.

Goodman, J. L., K.A. Moore and W.C. Dennison. 1995. Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon. Aquatic Botany **50**:37-47.

Griffin, K. 1997. Eelgrass ecology and commercial oyster cultivation in Tillamook Bay, Oregon. Tillamook Bay National Estuary Project Report #11-97.

Grosholz, E. D., G.M. Ruiz, C.A. Dean, K.A. Shirley, J.A. Maron, and P.G. Connors. 2000. The impacts of a nonindigenous marine predator in a California bay. Ecology **81**:1206-1224.

Harrison, P. G. 1987. Natural expansion and experimental manipulation of seagrass (*Zostera* spp.) abundance and the response of infaunal invertebrates. Estuarine, Coastal and Shelf Science **24**:799-812.

Harrison, P. G. 1990. Variations in success of eelgrass transplants over a five-years' period. Environmental Conservation **17**:157-163.

Heck, K. L., and R.J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. Pages 449-464 *in* V. S. Kennedy, editor. Estuarine perspectives. Academic Press, New York.

Holmer, M., and E. J. Bondgaard. 2001. Photosynthetic and growth response of eelgrass to low oxygen and high sulfide concentrations during hypoxic events. Aquatic Botany **70**:29-38.

Homziak, J., M.S. Fonseca and W.J. Kenworthy. 1982. Macrobenthic community structure in a transplanted eelgrass (*Zostera marina*) meadow. Marine Ecology Progress Series **9**:211-221.

Ingold, A., and D.C. Havill. 1984. The influence of sulphide on the distribution of higher plants in salt marshes. Journal of Ecology **72**:1043-1054.

Jones, C. G., J.H. Lawton and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos **69**:373-386.

Jones, C. G., J.H. Lawton and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology **78**:1946-1957.

Kaiser, M. J. 2001. Ecological effects of shellfish cultivation. Pages 51-75 *in* K. D. Black, editor. Environmental Impacts of Aquaculture. Sheffield Academic Press, Sheffield, UK.

Kruzynski, G. 2004. Cadmium in oysters and scallops: the BC experience. Toxicology Letters **148**:159-169.

Levi, F., and P. Francour. 2004. Behavioural response of *Mullus surmuletus* to havitat modification by the invasive macroalga *Caulerpa taxifolia*. Journal of Fish Biology **64**:55-64.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8**:133-137.

Loreto, M. L., M. Lara and J.J. Schmitter-Soto. 2003. Coral reef fish assemblages at Banco Chinchorro, Mexican Caribbean. Bulletin of Marine Science **73**:153-170.

Lubbers, L., W.R. Boynton, and W.M. Kemp. 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. Marine Ecology Progress Series **65**:1-14.

Marsh, G. A. 1973. The *Zostera* epifaunal community in the York River, Virginia. Chesapeake Science **14**:87-97.

Mistri, M. 2003. The non-indigenous mussel *Musculista senhousia* in an Adriatic lagoon: effects on benthic community over a ten year period. Journal of the Marine Biological Association of the United Kingdom **83**:1277-1278.

Mumby, P. J., A. J. Edwards, J. E. Arias-Gonzalez, K.C. Lindeman, P.G. Blackwell, A. Gall, M.L. Gorczynska, A. R. Harborne, C.L. Pescod, H. Renken, C. C. C. Wabnitz, and G. Llewellyn. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature **427**:533-536.

Murphy, M. L., S.W. Johnson, and D.J. Csepp. 2000. A comparison of fish assemblages in eelgrass and adjacent subtidal habitats near Craig, Alaska. Alaska Fishery Research Bulletin **7**:11-21.

Naylor, R. L., J. Eagle and W.L. Smith. 2003. Salmon aquaculture in the Pacific Northwest - a global industry. Environment **45**:18-39.

Nugues, M. 1996. Benthic community changes associated with intertidal oyster cultivation. Aquaculture Research **27**:913-924.

Orth, R., K.L. Heck, and J. Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries **7**:339-350.

Peralta, G., T.J. Bouma, J. vanSoelen, J.L. Perez-Llorens, and I. Hernandez. 2003. On the use of sediment fertilization for seagrass restoration: a mesocosm study on *Zostera marina* L. Aquatic Botany **75**:95-110.

Phillips, R. C. 1984. The ecology of eelgrass meadows in the Pacific Northwest: A community profile. U.S. Fish and Wildlife Service. FWS/OBS-84/24. 85 pp.

Quayle, D. 1964. Distribution of introduced marine mollusca in British Columbia waters. Journal of the Fisheries Research Board of Canada **21**:1155-1164.

Quayle, D. 1988. Pacific oyster culture in British Columbia. Canadian Bulletin of Fisheries and Aquatic Sciences **218**:241 p.

Reusch, T. B. H., and S.L. Williams. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. Oecologia **113**:428-441.

Ross, D. J., C.R. Johnson, C.L. Hewitt and G.M. Ruiz. 2004. Interaction and impacts of two introduced species on a soft-sediment marine assemblage in SE Tasmania. Marine Biology **144**:747-756.

Rudnick, D., T. Veldhuizen, R. Tullis, C. Culver, K. Hieb and B. Tsukimura. 2005. A life history model for the San Francisco Estuary population of the Chinese mitten crab, *Eriocheir sinensis* (Decapoda: Grapsoidea). Biological Invasions **7**:333-350.

Ruiz, G. M., P. Fofonoff, A.H. Hines, and E.D. Grosholz. 1999. Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. Limnology and Oceanography **44**:950-972.

Short, F. T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation **23**:17-27.

Smith, J. E., C.L. Hunter, E.J. Conklin, R. Most, T. Sauvage, C. Squair, and C.M. Smith. 2004. Ecology of the invasive red alga *Gracilaria salicornia* (Rhodophyta) on O'ahu, Hawai'i. Pacific Science **58**:325-343.

Sorokin, I.I., O. Giovanardi, F. Pranovi and P.I. Sorokin. 1999. Need for restricting bivalve culture in the southern basin of the Lagoon of Venice. Hydrobiologia **400**:141-148.

Trianni, M. S. 1996. The influence of commercial oyster culture activities on the benthic infauna of Arcata Bay. Humboldt State University, Humboldt, CA.

Truscott, J., J. Bones, C. Egan, G. Winterbottom and R. Paynter. 2005. Cortes Island Coastal Report for Shellfish Aquaculture. British Columbia Ministry of Sustainable Resource Management, Coast & Marine Planning Branch.

Waddell, J. E. 1964. The effect of oyster culture on eelgrass (*Zostera marina* L.) growth. MSc. Thesis. Humboldt State College, Humboldt, CA.

Waknitz, F. W., R.N. Iwamoto, and M.S. Strom. 2003. Interactions of Atlantic salmon in the Pacific Northwest IV. Impacts on the local ecosystems. Fisheries Research **62**:307-328.

Wilson, C. 2003. Shellfish to receive marketing boost. *in* Victoria Times-Colonist, Victoria, BC.

Wright, N. 2002. Eelgrass conservation for the B.C. coast: a discussion paper. B.C. Coastal Eelgrass Stewardship Project.

Wyllie-Echeverria, S., T. Mumford, J. Gaydos and S. Buffum. 2003. *Z. marina* declines in San Juan County, WA. Westcott Bay Taskforce Mini-Workshop.

EFFECTS OF NON-NATIVE OYSTER (*CRASSOSTREA GIGAS* THUNBERG) ON NATIVE EELGRASS (*ZOSTERA MARINA* L.) IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA

INTRODUCTION

Non-native species have invaded marine habitats worldwide. Many of these invasions have proven detrimental to native species, either directly through predation and competition, or indirectly through habitat modification (Carlton and Geller 1993, Carlton 1996, Reusch and Williams 1998, Crooks 2001, Branch and Steffani 2004, Ross et al. 2004). Many successful marine invaders act as ecosystem engineers by altering the physical conditions of their new habitat. These changes may lead to exclusion of native species (Jones *et al.* 1997, Coleman and Williams 2002, Lodge 1993). For example, the invasive alga *Caulerpa taxifolia* (Vahl) off the coast of France creates a homogeneous substrate matted with extensive rhizoids, leading to the decline of the native fish *Mullus surmuletus* (L.), which is unable to forage among the dense vegetation (Levi and Francour 2004). The Asian date mussel *Musculista senhousia* (Benson) modifies habitat by forming extensive mats that prevent deposit-feeding invertebrates from accessing sediment (Reusch and Williams 1998, Mistri 2003). The Mediterranean mussel *Mytilus galloprovincialis* (L.) forms dense beds on South African shores, excluding native limpets from rock surfaces (Branch and Steffani 2004).

Another such exotic species, the Pacific oyster (Ostreidae: *Crassostrea gigas* Thunberg), was introduced to coastal British Columbia, Canada, from Japan for aquaculture in the 1920s. Feral populations of the Pacific oyster established throughout

the Strait of Georgia when unusually warm water temperatures in 1932 and 1958 allowed successful spawning and strong oceanic currents aided dispersal (Quayle 1964, 1969). Today, feral and farmed populations spawn most years in late summer, although natural spawning is considered an insufficiently reliable source of spat for shellfish aquaculture (Quayle 1988, BCSGA 2003). The Pacific oyster is cultured in British Columbia using one of two methods: off-bottom tray culture or beach culture (BCSGA 2003). In the tray culture method, oysters are placed on large trays which are suspended from rafts or long lines in deep water (Quayle 1988, BCSGA 2003). In beach culture, oysters are grown directly on the sediment in the intertidal zone (Quayle 1988, BCSGA 2003). The shellfish aquaculture industry in British Columbia plans to increase oyster production from 7000 tonnes in 2003 to over 14,000 tonnes by 2007 (BCSGA 2003, Wilson 2003, DFO 2004). This increase in farmed populations, along with increasing global sea surface temperatures, means that another major breeding event would likely result in further range expansion of feral oysters.

A potential consequence of increased feral oyster distribution is the loss of native eelgrass (*Zostera marina* L.) beds. Oysters and eelgrass coexist at a regional scale in coastal British Columbia and the American Pacific Northwest, with oysters inhabiting the high-intertidal zone and eelgrass found in the low-intertidal to shallow subtidal zone (Dumbauld and Wyllie-Echeverria 2003, pers. obs.). However, coexistence is not observed at a fine scale: eelgrass is not found directly adjacent to oysters or in areas of former oyster culture, and eelgrass-free patches in the low-intertidal zone often correspond with oyster beds directly landward (Everett *et al.* 1995, pers. obs.). In addition, the presence of farmed oysters has been correlated with decreased eelgrass

abundance (Waddell 1964, Everett *et al.* 1995, Griffin 1997). This distribution suggests consistent impacts of oyster beds on eelgrass; however, the mechanisms behind these observed distributions are poorly understood and remain speculative (Everett *et al.* 1995, Griffin 1997).

The Pacific oyster differs from British Columbia's native oyster (*Ostrea lurida* Carpenter) in being larger and faster-growing, and having a higher filtering capacity and the ability to ingest a wide range of particle sizes (Quayle 1964, 1988). These characteristics make it both an ideal aquaculture organism and an ecologically significant invader. One potential pathway of interaction is that the presence of Pacific oyster affects eelgrass beds through accumulation of toxic levels of sulphide in sediments. Sediment sulphide concentration under cultured bivalves has been shown to be more than 100 times higher than at reference sites (Dahlback and Gunnarsson 1981, Grant *et al.* 1995). Eelgrass is highly susceptible to sulphides, showing decreased photosynthetic activity and slower growth at elevated sulphide concentrations (Goodman *et al.* 1995, Holmer and Bondgaard 2001). Through promotion of a sulphide-rich substrate, Pacific oyster beds (cultured or feral) may be linked to local eelgrass loss.

Because eelgrass provides habitat for many fish and invertebrate species, loss of eelgrass would likely result in substantial changes to intertidal and subtidal community structure. Eelgrass beds are characterized by high primary productivity, sediment stability, habitat complexity, reduced wave action and protection from predators (Orth *et al.* 1984, Phillips 1984, Everett *et al.* 1995, Trianni 1996, Coleman and Williams 2002, Duarte 2002). On the Pacific coast of North America, eelgrass beds act as nurseries for juveniles of many commercially and ecologically important organisms such as salmonids

and crabs, and as egg attachment sites for herring (Orth *et al.* 1984, Griffin 1997, Murphy *et al.* 2000, Wyllie-Echeverria *et al.* 2003). Zooplankton and detritus trapped in eelgrass beds due to lower current velocity serve as food for juvenile fish and invertebrates (Griffin 1997). Infaunal organisms are protected from predators by eelgrass root structure (Reise 1985), while eelgrass leaves provide refuge for juvenile crabs and myriad other motile epifaunal organisms (Orth and vanMontfrans 1982, Fernandez *et al.* 1993). The shift from eelgrass-dominated to oyster-dominated tidal flats may represent a reduction in habitat quality for many species, leading to changes in community composition. For instance, fish and decapod predation on macrofauna is higher in tidal flats dominated by oysters than in those dominated by eelgrass (Reise 1985, Castel *et al.* 1989), and overall benthic macrofauna abundance is reduced in oyster-dominated habitats due to the accumulation of hypoxic sediments (Castel *et al.* 1989).

This experiment was conducted to test the hypothesis that high sulphide levels below Pacific oyster beds are the result of oyster presence, and that conditions below oyster beds are inhospitable to recolonisation by eelgrass.

METHODS

Study sites

All study sites were located on the southwest coast of Cortes Island, British Columbia, Canada (50°4′N, 124°56′W). Eelgrass transplants were performed at sites 1-3 (Fig 2-1). Each transplant site consisted of an area immediately below an oyster bed (the 'below-oyster' zone), and the eelgrass bed adjacent to this area (Fig. 2-2). Substantial recreational boat traffic was present in July and August at Site 1 due to proximity to

Manson's Bay and the government dock at Manson's Landing Provincial Park. Oyster transplants were performed at sites 4 and 5 (Fig 2-1).

Eelgrass transplants

A 20 m transect was placed parallel to shore at each study site so that 10 m of the transect was in the eelgrass bed and the other 10 m was in the below-oyster zone (Fig 2-3). The transect line was placed as high as possible within the *Z. marina* zone to maximize accessibility and proximity to the oyster bed.

Every 1 m along the transect line, a 15 cm deep hole was excavated using a 10 cm diameter PVC pipe (Phillips 1990). Cores of *Z. marina* (15 cm deep, 10 cm diameter) were taken from randomly-chosen points along an additional line located about 2 m seaward from the 20 m transect line, and used to fill the holes along the 20 m transect line (Fig.2-3). Original sediment from donor cores was kept intact for transplanting (Phillips 1990). A wire-stemmed flag was used to mark the location of each transplant.

The number of shoots (leaf bundles) and individual leaves in each transplant were counted by placing a 10 cm diameter plastic ring around the transplanted core, using the flag as a guideline for positioning. Shoot and leaf counts were recorded immediately after transplanting, and at five subsequent sampling events for Site 1, four subsequent sampling events for Site 2, and two subsequent sampling events for Site 3.

Oyster transplants

Twenty-four 0.25 m^2 plots were set up in the eelgrass bed at each of the two oyster transplant sites. Plots were arranged in three rows of eight plots running parallel to shore, with edges of each plot at least 1.5 m from all other plots (Fig 2-4). There were four treatments: high density live oysters (24 oysters per plot), low density live oysters

(12 oysters per plot), low density oyster shells (12 empty shells held shut with plastic cable ties) and control (empty plot). High and low densities were based on preliminary field surveys of oyster density at the centre and edge, respectively, of feral oyster beds. Empty oyster shells were used to control for abiotic effects of oyster shells on eelgrass health, such as changes to water flow. Each oyster transplant site consisted of 6 plots of high density live oysters, 10 of low density live oysters, 4 of oyster shells and 4 control plots. Treatments were randomly distributed among plots.

At 4 weeks and 10 weeks after setup, each oyster-transplant plot was sampled for sediment sulphide concentration. Samples of sediment porewater were drawn using a 60 cc syringe from the seaward edge of each plot and at 1 m below the seaward edge of each plot, at a depth of 10 cm below the sediment surface. Samples were stored on ice and analyzed within 1 h of collection to minimize oxidation (Cline 1969). Sulphide concentration was measured using a Hach DR2400 portable spectrophotometer.

Using the same protocol, sulphide concentration was also measured in the eelgrass bed and below-oyster zone at Sites 2 and 3. Sixteen samples were taken from each eelgrass bed and 10 samples were taken from each below-oyster zone.

Statistical methods

Number of shoots and leaves in eelgrass-bed transplants and below-oyster transplants were compared over time using repeated-measures ANOVA in the SAS 8.2 software package (SAS 2001).

Using the SPSS 11.5 software package, repeated-measures ANOVA was used to compare sediment sulphide concentrations over time among the 4 different treatments in the oyster transplant experiment (SPSS 2002). Nested ANOVA was used to assess

differences in sediment sulphide concentrations between the eelgrass bed and below-oyster zone (SPSS 2002).

RESULTS

Eelgrass transplant

Over time, the number of shoots and leaves in cores transplanted within the eelgrass bed was significantly greater than in cores transplanted to below-oyster zones at all sites (shoots $p=0.0009$, leaves $p=0.0004$; Table 2-1). While number of leaves per transplant in below-oyster transplants decreased over the course of the experiment, number of leaves per transplant in eelgrass bed transplants increased over time. Time, treatment and the interactive effect of time and treatment all significantly affected the number of shoots and leaves at all sites ($p<0.05$ for all tests; Table 2-1). Site had a significant effect on number of shoots and leaves (shoots $p<0.0001$, leaves $p=0.0008$); however, there was no significant interactive term of site, treatment and time ($p=0.5220$), indicating that the interactive effect of treatment and time was not affected by site (Table 2-1).

Mean number of shoots and leaves per transplanted core declined until the end of July in both treatments at all sites (Fig. 2-5, 2-6). In August, the number of shoots had recovered completely in both eelgrass bed and below-oyster transplants at Site 3, and in the eelgrass bed transplants at Site 2 (Fig 2-5). Number of leaves recovered only in eelgrass bed transplants at Sites 2 and 3 (Fig 2-6). Observations at Site 1 were discontinued after measurements were taken on 31 July because all plots in the below-oyster zone were completely devoid of eelgrass and very few shoots remained in the eelgrass-bed transplants. The eelgrass bed at Site 1 appeared to have experienced

substantial physical damage (likely due to boat traffic) between 15 July and 31 July, as density of *Z. marina* was drastically reduced intertidally and appeared somewhat reduced subtidally.

The abundance of green filamentous algae (*Enteromorpha intestinalis* L.) varied over time and among sites, but over the course of the summer, slightly more *E. intestinalis* was present near below-oyster zone transplants than near eelgrass bed transplants (Table 2-2). Thick mats of *E. intestinalis* were present in the below-oyster zone at Site 1 in late June, and in the eelgrass bed at Site 2 in early July (Table 2-2).

Oyster transplant

Sulphide concentrations measured in the oyster transplant experiment ranged from 0-80 μg/L but no relationship between treatment (high-density live oysters, low-density live oysters, empty oyster shells, and untreated controls) and sulphide concentration was found (all $p>0.3$). No significant difference was found between measurements taken at the edge of the plot and those taken 1 m seaward of the plot edge ($p >0.2$ for both sites). No differences in epiphyte load were observed among treatments.

Average sulphide concentration in the below-oyster zone was 117.25 μg /L (N=20; SE=15.89), significantly greater than average sulphide concentration in the adjacent eelgrass beds (17.34 μg/L; N=32, SE =2.63) ($p = 0.001$, Fig 2-7).

DISCUSSION

Results of the eelgrass transplant experiment indicate that the below-oyster zone is a poor habitat for eelgrass; oyster presence in the high-intertidal was correlated with high sulphide concentrations in the low-intertidal, suggesting that sulphide toxicity is a

possible mechanism for eelgrass loss below oyster beds. Over the course of the eelgrass transplant experiment, leaf number increased in cores transplanted to eelgrass beds and decreased in cores transplanted below oyster beds. After an initial decrease in shoot density in all eelgrass transplants, those transplanted to an eelgrass bed experienced a more rapid increase than those transplanted to the below-oyster zone. No detectable sulphide accumulation occurred below transplanted oysters over the experimental period.

Results of other research suggest that sulphide accumulation may be responsible for the inability of eelgrass to establish or maintain itself below oysters. Dense populations of filter-feeding bivalves such as oysters can cause a marked increase in organic content of the sediment by depositing large quantities of feces and pseudofeces (Castel *et al.* 1989, Nugues 1996, Sorokin *et al.* 1999, Kaiser 2001). These deposits of organic material cause increased local oxygen demand by aerobic microbes, leading to hypoxic sediment conditions that promote the growth of sulphate-reducing bacteria (Ingold and Havill 1984, Castel *et al.* 1989, deZwaan and Babarro 2001). These bacteria release sulphide into the sediment as a metabolic by-product, resulting in high concentrations of sediment sulphide (Howes *et al.* 1984, Ingold and Havill 1984, Sorokin *et al.* 1999). I found elevated sulphide concentrations in the below-oyster zone as compared to an eelgrass bed, similar to findings of others (Dahlback and Gunnarsson 1981, Sorokin *et al.* 1999). Sulphide toxicity to eelgrass has been demonstrated by decreased photosynthesis, increased respiration, and meristematic cell decay following sulphide exposure (Goodman *et al.* 1995, Holmer and Bondgaard 2001). Therefore the deposition of organic matter by oysters and subsequent accumulation of sulphide in the

sediment may explain the significantly decreased growth and survival of eelgrass transplanted to the below-oyster zone.

The initial decrease in leaf count and shoot density for all eelgrass transplants may have been due to transplanting stress, or transplants may have coincided with other factors contributing to eelgrass decline. Annual variation in eelgrass abundance occurs due to changes in nutrient availability, temperature, turbidity and salinity as well as physical disturbances (Phillips 1984, Kentula and McIntire 1986). Because eelgrass typically dies off in fall and winter and grows dramatically in spring and summer, it is unlikely that initial decreases in leaf count and shoot density were due to seasonal growth patterns (Phillips 1984, Kentula and McIntire 1986).

The dramatic changes in algal cover that were observed in eelgrass beds and below-oyster areas may have affected eelgrass health: heavy algal cover was likely sufficient to block light for photosynthesis, while light algal cover may have provided protection from desiccation at low tide. Harrison (1987) found that *Z. marina* seedlings took at least a year from transplanting to reach peak shoot density because of the time required to recover from transplant shock and re-establish roots. Monitoring of non-transplanted eelgrass density for the duration of the transplant experiment would be required to distinguish between these hypotheses. Regardless of the reason for the initial post-transplanting decline, the decline was more pronounced in eelgrass transplanted to the below-oyster zone at all sites, and recovery of eelgrass transplanted to the below-oyster zone was significantly poorer than that of cores transplanted in the eelgrass bed at sites 2 and 3.

Although other studies have found high concentrations of sulphide directly beneath established cultures of oysters (Castel *et al.* 1989) and other bivalves (Dahlback and Gunnarsson 1981, Sorokin *et al.* 1999), the oyster transplant experiment showed no accumulation of sediment sulphide at the seaward edge of transplanted oyster plots, and no significant differences between treatments. The length of the experimental period may have been too short for a measurable concentration of sulphide to have developed, especially given the indirect microbial pathway by which sulphide accumulates below bivalve cultures (Dahlback and Gunnarsson 1981, Howes *et al.* 1983, Ingold and Havill 1984, Castel *et al.* 1989, Sorokin *et al.* 1999). It is also possible that the size of the oyster transplant plots was too small to have produced the anoxia that is a precursor to sulphide accumulation, since deposition of large amounts organic matter in other studies resulted from extensive, high-density bivalve cultures (Dahlback and Gunnarsson 1981, Castel *et al.* 1989, Sorokin *et al.* 1999). Future research should focus on larger oyster transplants over a longer period of time; long-term monitoring of sulphide and organic carbon in sediment below new ground-culture oyster farms would likely yield the most informative results.

The results of this study provide insight into interactions between introduced oysters and native eelgrass. Because eelgrass tends to grow in areas considered ideal for oyster aquaculture, and because the oyster aquaculture industry continues to expand, such interactions may occur throughout coastal British Columbia and the American Pacific Northwest (Everett *et al.* 1995, Simenstad and Fresh 1995, Griffin 1997). The eelgrass transplant experiment employed seagrass restoration protocols common in conservation projects (Harrison 1990, Phillips 1990) and demonstrated their ineffectiveness for

restoring *Z. marina* below oyster beds on Cortes Island. Therefore, the best strategy for minimizing the effects of oyster aquaculture on native eelgrass may be to limit beach-culture leases to areas without eelgrass, and to prevent establishment of feral oyster beds.

Eelgrass faces many anthropogenic threats in addition to the effects of introduced oysters. Substantial losses of seagrass have been documented in Australia (Kendrick *et al.* 2002), along the East coast of the United States (Short and Burdick 1996), and along the West coast of North America in Washington (Wyllie-Echeverria *et al.* 2003) and British Columbia (Wright 2002). A variety of human-induced disturbances such as dredging, eutrophication from agricultural runoff, and industrial waste spills, as well as natural disturbances such as extreme weather conditions, grazing and sediment resuspension, have been cited as causes of seagrass declines (Short and Wyllie-Echeverria 1996, Wright 2002, Wyllie-Echeverria *et al.* 2003). The cumulative effects of such factors, in addition to the planned increases to shellfish aquaculture, could exacerbate eelgrass loss in British Columbia and the American Pacific Northwest.

Non-native species such as the Pacific oyster can profoundly affect ecosystem function in their new environment. Little experimental work has been done on the effects of oysters on native eelgrass beds (Waddell 1964, Castel *et al.* 1989, Everett *et al.* 1995), although correlation between oyster presence and eelgrass loss has been noted (Waddell 1964, Everett et al. 1995). The results of this study indicate that eelgrass cannot be re-established below oyster beds simply by transplanting; a more sophisticated means of restoration is required (perhaps aimed at reducing sulphides in sediments), or we may face permanent long-term reductions in seagrass due to the spread of Pacific oysters. Further research into the mechanisms responsible for eelgrass absence below oyster beds

is required, as it is likely that many interactive effects, including sulphide accumulation, contribute to eelgrass-oyster interactions.

TABLES AND FIGURES

Table 2-1. Results of repeated measures ANOVA for each eelgrass transplant site. *Site* and *Treatment* (i.e. transplanted to eelgrass or below-oyster zone) are between-subjects and *Time* is a within-subjects effect.

Site	Effect	Measure	P
1	Treatment	Shoots	0.0575
		Leaves	0.0086
	Time	Shoots	<0.0001
		Leaves	<0.0001
	Time * Treatment	Shoots	0.0107
		Leaves	0.0003
2	Treatment	Shoots	0.0168
		Leaves	0.0109
	Time	Shoots	0.0002
		Leaves	<0.0001
	Time * Treatment	Shoots	<0.0001
		Leaves	<0.0001
3	Treatment	Shoots	0.0137
		Leaves	0.0137
	Time	Shoots	0.0003
		Leaves	<0.0001
	Time * Treatment	Shoots	<0.0001
		Leaves	<0.0001
All	Site	Shoots	<0.0001
		Leaves	0.0008
	Treatment	Shoots	0.0009
		Leaves	0.0004
	Site * Treatment	Shoots	0.8053
		Leaves	0.7682
	Time	Shoots	<0.0001
		Leaves	<0.0001
	Site * Time	Shoots	0.3223
		Leaves	0.9422
	Treatment * Time	Shoots	<0.0001
		Leaves	<0.001
	Site * Treatment * Time	Shoots	0.2870
		Leaves	0.5220

Table 2-2. Relative abundance of green alga *E. intestinalis* at eelgrass transplant sites. (-) indicates no visible *E. intestinalis*; (+) indicates scattered *E. intestinalis*; (++) indicates a thin layer of *E. intestinalis* through which light could pass; (+++) indicates a mat of *E. intestinalis* sufficiently thick to block light. Site 1 observations were discontinued on 31 July because all plots in the below-oyster zone were completely devoid of eelgrass.

	Site 1		Site 2		Site 3	
	Eelgrass	Below oy.	Eelgrass	Below oy.	Eelgrass	Below oy.
June	6th: - 18th: ++ 30th: +	6th: + 18th : +++ 30th: +++	29th: +	29th: +	n/a	n/a
July	15th: - 31st: +	15th: - 31st: +	4th: +++ 14th: +	4th: ++ 14th: +	18th: +	18th: +
August	n/a	n/a	2nd: + 29th: +	2nd: ++ 29th: ++	2nd: + 29th: -	2nd: + 29th: -

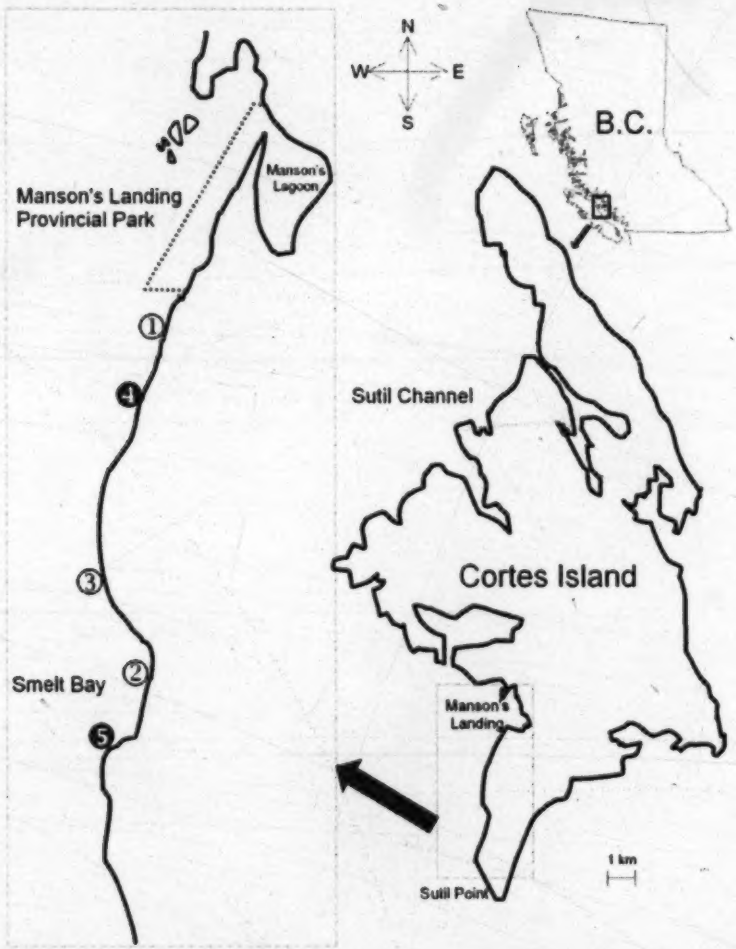

Figure 2-1. Map of Cortes Island with detail of study site locations. Unfilled circles indicate eelgrass transplant experiment sites; filled circles indicate oyster transplant experiment sites. Transplant Site 1 was located in the low-intertidal zone below a feral oyster bed. Beach-culture oyster farms are present south of Site 1, while eelgrass beds are found along the shore north and south of Site 1. Transplant Sites 2 and 3 were located in Smelt Bay, north of Smelt Bay Provincial Park. Eelgrass is found in large patches throughout Smelt Bay. A feral oyster bed was located in the high-intertidal above Site 2, whereas the below-oyster zone at Site 3 was located below a beach-culture oyster farm. Site 4 was an eelgrass bed located approximately 500 m south of Manson's Landing Provincial Park. Ground-culture oyster leases were located in the high-intertidal directly north and south of Site 4. Site 5 was an eelgrass bed located in Smelt Bay with a feral oyster bed in the high-intertidal directly to the north but no oysters directly to the south. No oysters were present in the high-intertidal directly above the eelgrass beds.

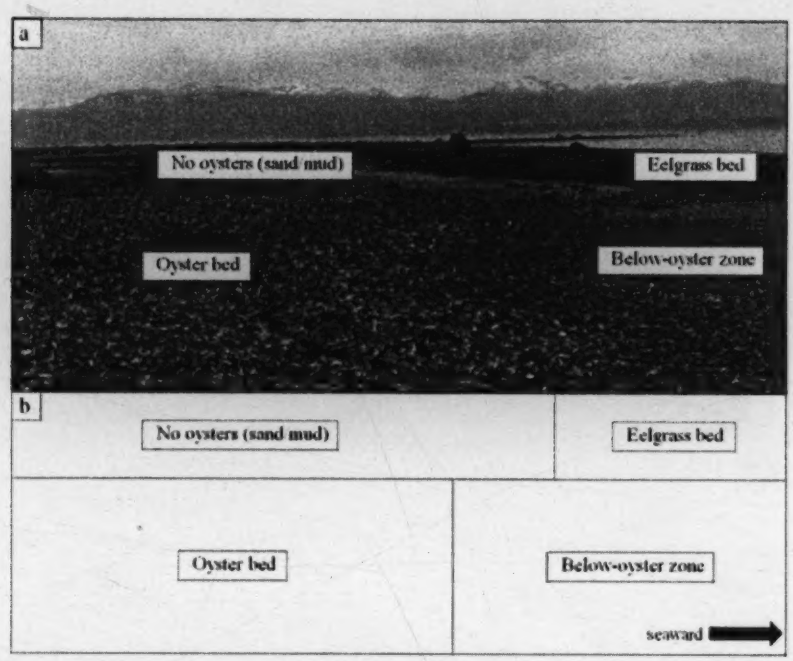

Figure 2-2. Study site layout. (a) shows physical relationship of below-oyster zone to oyster bed and eelgrass bed. (b) shows schematic diagram of below-oyster zone, oyster bed and eelgrass bed.

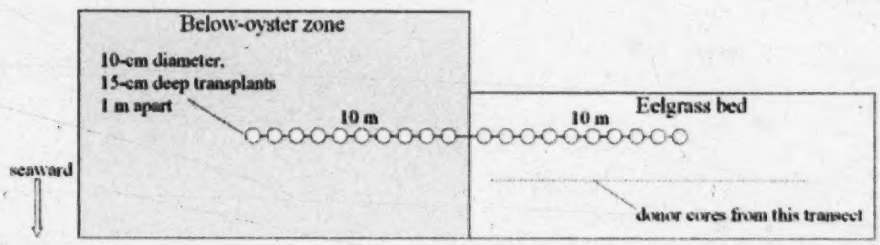

Figure 2-3. Schematic diagram of eelgrass transplant experiment (not to scale). Unfilled circles represent transplanted eelgrass cores.

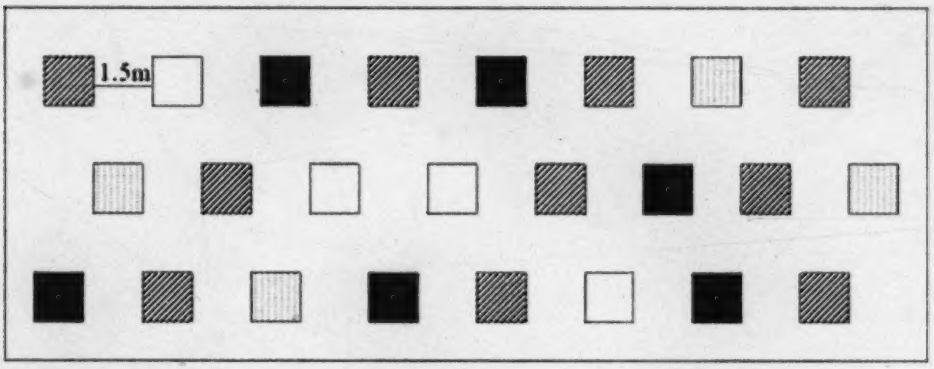

Figure 2-4. Schematic diagram of oyster transplant experiment (not to scale). Squares represent 0.5 m x 0.5 m experimental plots. Filled squares represent high-density oyster plots (24 oysters/plot); diagonally shaded squares represent low-density oyster plots (12 oysters/plot); stippled squares represent empty-shell plots (12 shells/plot); unfilled squares represent undisturbed control plots. Plots were a minimum of 1.5 m apart from the next closest plot in all directions.

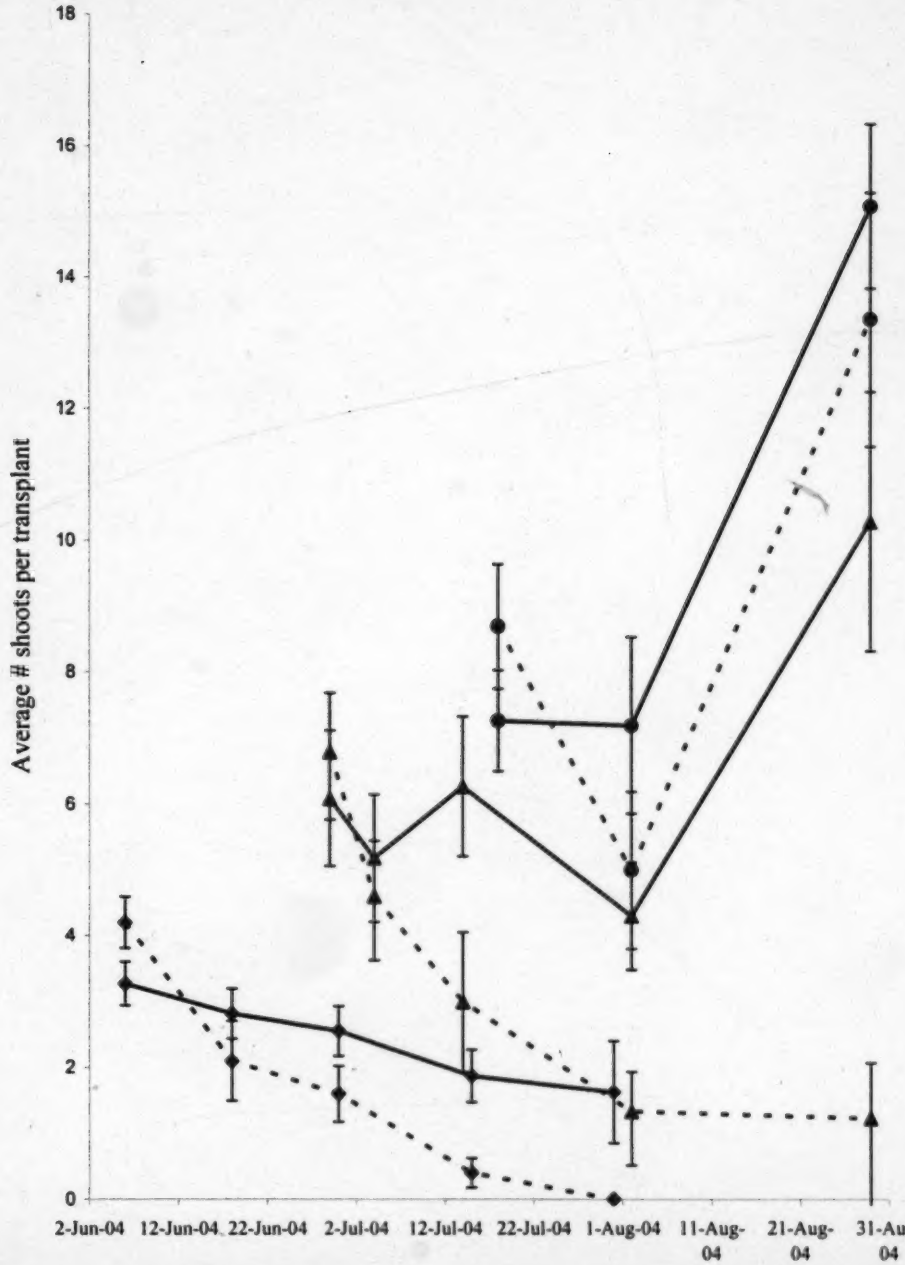

Figure 2-5. Change in average number of shoots per transplant over time in eelgrass and below-oyster zone. Solid lines represent eelgrass bed transplants; dotted lines represent below-oyster transplants. ◆ indicates Site 1 transplants, ▲ indicates Site 2 transplants, and ● indicates Site 3 transplants.

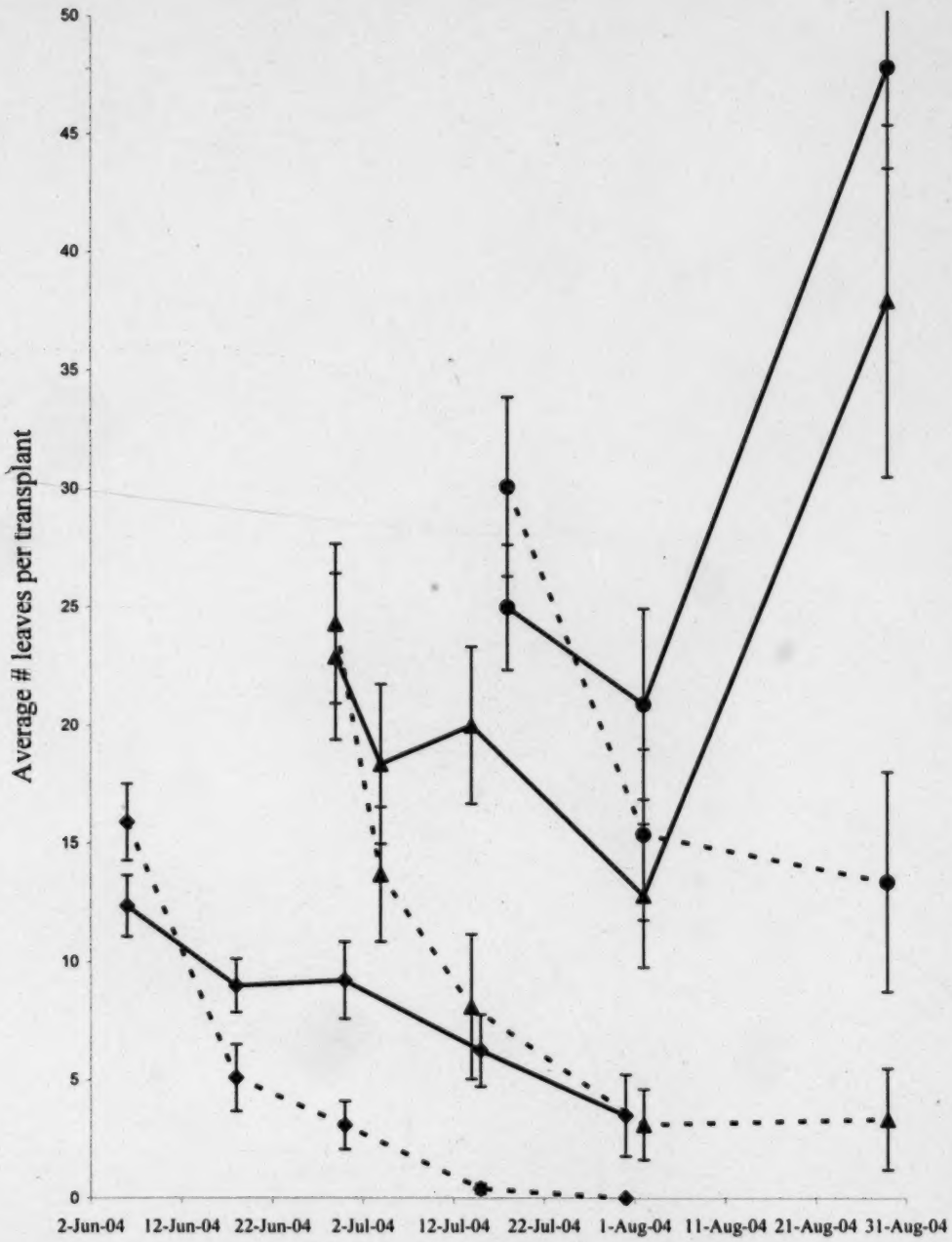

Figure 2-6. Change in average number of leaves in eelgrass transplants over time in eelgrass and below-oyster zone. Solid lines represent eelgrass bed transplants; dotted lines represent below-oyster transplants. ◆ indicates Site 1 transplants, ▲ indicates Site 2 transplants, and ● indicates Site 3 transplants.

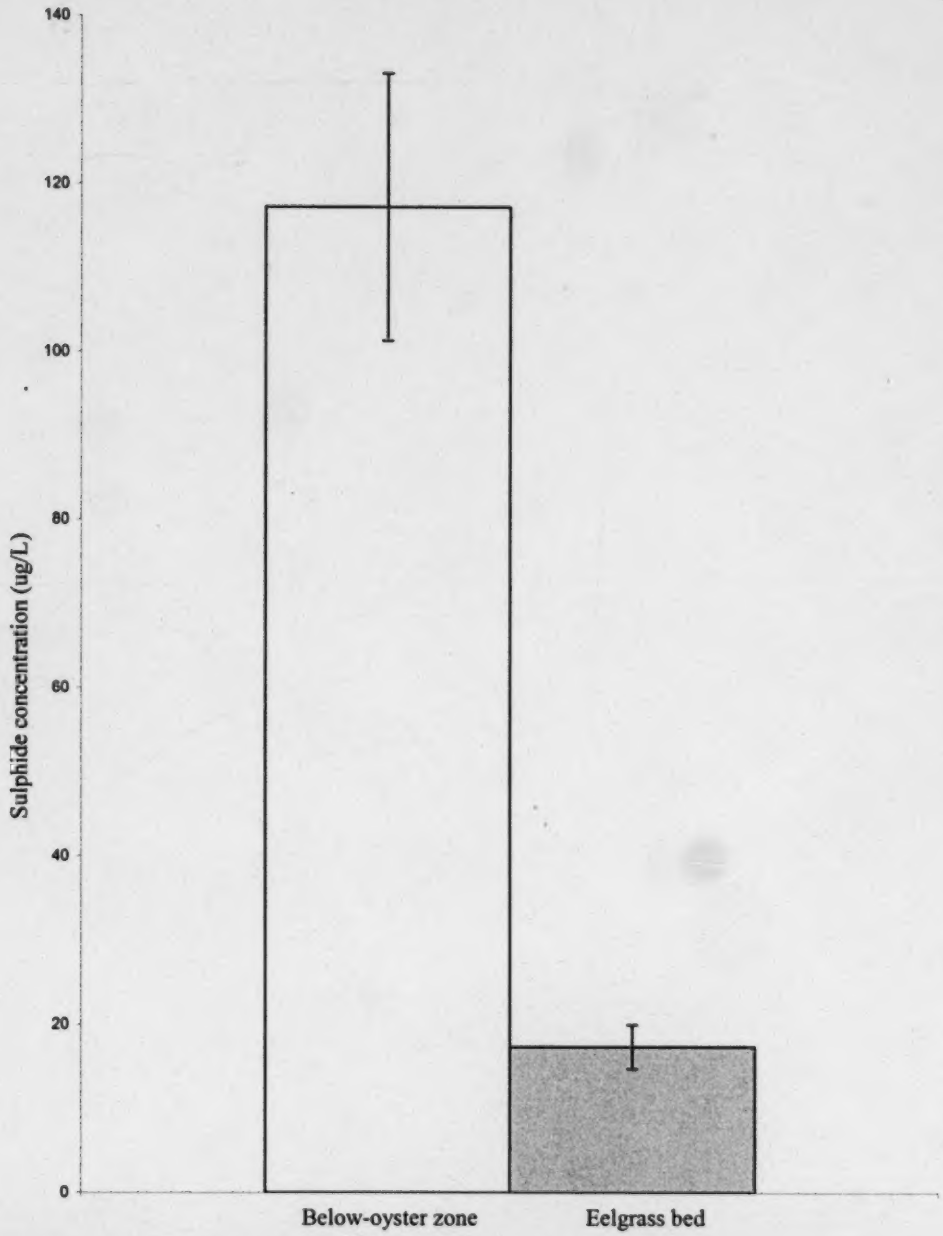

Figure 2-7. Sediment sulphide concentrations in below-oyster zone and eelgrass bed. Results represent pooled data from 2 eelgrass beds (16 samples each) and 2 below-oyster zones (10 samples each). Error bars = SE.

REFERENCES

BCSGA. 2003. Information resource centre. BC Shellfish Growers Association http://www.bcsga.ca. Accessed 21 Feb 2005.

Branch, G. M., and C. N. Steffani. 2004. Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). Journal of Experimental Marine Biology and Ecology **300**:189-215.

Carlton, J. T. 1996. Pattern, process and prediction in marine invasion ecology. Biological Conservation **78**:97-106.

Carlton, J. T., and J.B. Geller. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. Science **261**:78-82.

Castel, J., J-P. Labourg, V. Escaravage, I. Auby, and M.E. Garcia. 1989. Influence of seagreass beds and oyster parks on the abundance and biomass patterns of meio- and macrobenthos in tidal flats. Estuarine, Coastal and Shelf Science **28**:71-85.

Cline, J. D. 1969. Spectrophotometric determination of hydrogen sulfide in natural waters. Limnology and Oceanography **14**:454-458.

Coleman, F. C., and S.L Williams. 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends in Ecology and Evolution **17**:40-44.

Crooks, J. A. 2001. Assessing invader roles within changing ecosystems: historical and environmental perspectives on an exotic mussel in an urbanized lagoon. Biological Invasions **3**:23-26.

Dahlback, B., and L.A.H. Gunnarsson. 1981. Sedimentation and sulfate reduction under a mussel culture. Marine Biology **63**:269-275.

deZwaan, A., and J.M.F. Babarro. 2001. Studies on the causes of mortality of the estuarine bivalve *Macoma balthica* under conditions of (near) anoxia. Marine Biology **138**:1021-1028.

DFO (Department of Fisheries and Oceans). 2004. 2003 Canadian aquaculture production statistics. Fisheries and Oceans Canada, http://www.dfo-mpo.gc.ca/communic/statistics/aqua/aqua03_e.htm. Accessed 25 April 2005.

Duarte, C. M. 2002. The future of seagrass meadows. Environmental Conservation **29**:192-206.

Dumbauld, B. R., and S. Wyllie-Echeverria. 2003. The influence of burrowing thalassinid shrimps on the distribution of intertidal segrasses in Willapa Bay, Washington, USA. Aquatic Botany **77**:27-42.

Everett, R., GM Ruiz, and JT Carlton. 1995. Effect of oyster mariculture on submerged aquatic vegetation - an experimental test in a Pacific Northwest estuary. Marine Ecology Progress Series **125**:205-217.

Fernandez, M., O. Iribarne, and D. Armstrong. 1993. Habitat selection by young-of-the-year Dungeness crab, *Cancer magister*, and predation risk in intertidal habitats. Marine Ecology Progress Series **92**:171-177.

Goodman, J. L., K.A. Moore and W.C. Dennison. 1995. Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon. Aquatic Botany **50**:37-47.

Grant, J., A Hatcher, D.B. Scott, P. Pocklington, C.T. Shafer, and G.V. Winters. 1995. A multidisciplinary approach to evaluating impacts of shellfish aquaculture on benthic communities. Estuaries **18**:124-144.

Griffin, K. 1997. Eelgrass ecology and commercial oyster cultivation in Tillamook Bay, Oregon. Tillamook Bay National Estuary Project Report #11-97.

Harrison, P. G. 1987. Natural expansion and experimental manipulation of seagrass (*Zostera spp.*) abundance and the response of infaunal invertebrates. Estuarine, Coastal and Shelf Science **24**:799-812.

Harrison, P. G. 1990. Variations in success of eelgrass transplants over a five-years' period. Environmental Conservation **17**:157-163.

Holmer, M., and E. J. Bondgaard. 2001. Photosynthetic and growth response of eelgrass to low oxygen and high sulfide concentrations during hypoxic events. Aquatic Botany **70**:29-38.

Howes, B.L., J.W.H. Dacey, and D.M. King. 1984. Carbon flow through oxygen and sulfate reduction pathways in salt marsh sediments. Limnology and Oceanography **29**: 1037-1051.

Ingold, A., and D.C. Havill. 1984. The influence of sulphide on the distribution of higher plants in salt marshes. Journal of Ecology **72**:1043-1054.

Jones, C. G., J.H. Lawton and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology **78**:1946-1957.

Kaiser, M. J. 2001. Ecological effects of shellfish cultivation. Pages 51-75 *in* K. D. Black, editor. Environmental Impacts of Aquaculture. Sheffield Academic Press, Sheffield, UK.

Kendrick, G. A., M. J. Aylward, B. J. Hegge, M. L. Cambridge, K. Hillman, A. Wyllie, and D. A. Lord. 2002. Changes in seagrass coverage in Cockburn Sound, Western Australia between 1967 and 1999. Aquatic Botany **73**:75-87.

Kentula, M.E., and C.D. McIntire. 1986. The autoecology and production dynamics of eelgrass (*Zostera marina* L.) in Netarts Bay, Oregon. Estuaries **9**:188-199.

Levi, F., and P. Francour. 2004. Behavioural response of *Mullus surmuletus* to habitat modification by the invasive macroalga *Caulerpa taxifolia*. Journal of Fish Biology **64**:55-64.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8**:133-137.

Mistri, M. 2003. The non-indigenous mussel *Musculista senhousia* in an Adriatic lagoon: effects on benthic community over a ten year period. Journal of the Marine Biological Association of the United Kingdom **83**:1277-1278.

Murphy, M. L., S.W. Johnson, and D.J. Csepp. 2000. A comparison of fish assemblages in eelgrass and adjacent subtidal habitats near Craig, Alaska. Alaska Fishery Research Bulletin **7**:11-21.

Nugues, M. 1996. Benthic community changes associated with intertidal oyster cultivation. Aquaculture Research **27**:913-924.

Orth, R., K.L. Heck, and J. Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries **7**:339-350.

Orth, R., and J. vanMontfrans. 1982. Structural analysis of benthic communities associated with vegetated and unvegetated habitats. Pages 232 pp. *in* R. J. Orth, and J. vanMontfrans, editor. Interactions of Resident Consumers in a Temperate Estuarine Seagrass Community: Vaucluse Shores, Virginia, USA. Virginia Institute of Marine Sciences.

Phillips, R. C. 1984. The ecology of eelgrass meadows in the Pacific Northwest: A community profile. U.S. Fish and Wildlife Service. FWS/OBS-84/24. 85 pp.

Phillips, R. C. 1990. Transplant methods. Pages 51-54 *in* R. C. Phillips, and C.P. McRoy, editor. Seagrass research methods. UNESCO, Paris, France.

Quayle, D. 1964. Distribution of introduced marine mollusca in British Columbia waters. Journal of the Fisheries Research Board of Canada **21**:1155-1164.

Quayle, D. 1969. Pacific oyster culture in British Columbia. Fisheries Research Board of Canada Bulletin.

Quayle, D. 1988. Pacific oyster culture in British Columbia. Canadian Bulletin of Fisheries and Aquatic Sciences **218**:241 p.

Reise, K. 1985. Tidal Flat Ecology. Springer-Verlag, Berlin. 191 pp.

Reusch, T. B. H., and S.L. Williams. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. Oecologia **113**:428-441.

Ross, D. J., C.R. Johnson, C.L. Hewitt and G.M. Ruiz. 2004. Interaction and impacts of two introduced species on a soft-sediment marine assemblage in SE Tasmania. Marine Biology **144**:747-756.

SAS. 2001. SAS System for Windows, Version 8.2, SAS Institute, Cary, NC.

Short, F. T., and D.M. Burdick. 1996. Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, Massachusetts. Estuaries **19**:730-739.

Short, F. T., and S. Wyllie-Echeverria. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation **23**:17-27.

Simenstad, C., and K.I. Fresh. 1995. Influence of intertidal aquaculture on benthic communities in Pacific Northwest estuaries: scales of disturbance. Estuaries **18**:43-70.

Sorokin, I. I., O. Giovanardi, F. Pranovi and P.I. Sorokin. 1999. Need for restricting bivalve culture in the southern basin of the Lagoon of Venice. Hydrobiologia **400**:141-148.

Trianni, M. S. 1996. The influence of commercial oyster culture activities on the benthic infauna of Arcata Bay. Humboldt State University, Humboldt, CA.

Waddell, J. E. 1964. The effect of oyster culture on eelgrass (*Zostera marina* L.) growth. MSc. Thesis. Humboldt State College, Humboldt, CA.

Wilson, C. 2003. Shellfish to receive marketing boost. *in* Victoria Times-Colonist, Victoria, BC.

Wright, N. 2002. Eelgrass conservation for the B.C. coast: a discussion paper. B.C.

Coastal Eelgrass Stewardship Project.

Wyllie-Echeverria, S., T. Mumford, J. Gaydos and S. Buffum. 2003. *Z. marina* declines in San Juan County, WA. Westcott Bay Taskforce Mini-Workshop.

DISPLACEMENT OF NATIVE EELGRASS (*ZOSTERA MARINA* L.) BY INTRODUCED OYSTERS (*CRASSOSTREA GIGAS* THUNBERG) SIGNIFICANTLY ALTERS INTERTIDAL COMMUNITY STRUCTURE

INTRODUCTION

Many organisms create, modify or maintain habitats through their morphology or behaviour (Jones *et al.* 1994, 1997, Coleman and Williams 2002). Organisms that directly or indirectly control other species' access to resources through physical processes have been called "ecosystem engineers" (Jones *et al.* 1997). Marine ecosystem engineers include reef-forming corals, mangroves, mussels and seagrasses, all of which increase habitat complexity and support diverse assemblages of fish, invertebrates and algae (Coleman and Williams 2002, Loreto *et al.* 2003, Mumby *et al.* 2004).

Seagrass beds act as ecosystem engineers due to their physical structure, which provides refuge from predation, stabilizes sediments, slows ocean currents and traps planktonic larvae and suspended particulate matter (Jones *et al.* 1994, Coleman and Williams 2002). The diversity and abundance of fish and invertebrates associated with eelgrass (*Zostera marina* L.) beds are frequently attributed to these physical characteristics (Marsh 1973, Heck and Orth 1980, Lubbers *et al.* 1990, Griffin 1997). In coastal British Columbia and the Pacific Northwest of the United States, eelgrass beds serve as habitat for juvenile salmon (*Oncorhynchus* spp.) and spawning grounds for Pacific herring (*Clupea harengus* L.) (Reise *et al.* 1989, Griffin 1997, Murphy *et al.* 2000, Sheridan and Minello 2003, Wyllie-Echeverria *et al.* 2003). The suspended particulate matter and planktonic organisms trapped by eelgrass blades nourish many

suspension-feeding invertebrates, and promote the development of distinct eelgrass-associated epibenthic and epifaunal assemblages (Marsh 1973, Lubbers *et al.* 1990, Griffin 1997). In turn, these complex invertebrate assemblages provide prey for crabs and fish (Marsh 1973, Trianni 1996). A diverse infaunal assemblage is protected against large epibenthic predators by eelgrass root and rhizome structure (Summerson and Peterson 1984, Reise 1985).

In coastal British Columbia and the Pacific Northwest, eelgrass beds co-exist regionally with the Pacific oyster (*Crassostrea gigas* Thunberg). *C. gigas* was introduced from Japan in the early 20th century for aquaculture, and has since become a prominent feature of the intertidal zone in many areas (Quayle 1964). Oyster beds on the West coast of North America occur as either beach-cultivated sites, in which oysters are grown directly on the substrate in the intertidal zone (BCSGA 2003), or as feral oyster beds, which have resulted from spawning of cultured oysters (Quayle 1964, Dumbauld *et al.* 2001).

Like many successful invaders, the Pacific oyster alters the physical conditions of its new environment, and thereby also acts as an ecosystem engineer (Lodge 1993). Oysters change water flow, increase habitat complexity in the high-intertidal zone, add large quantities of organic matter to the sediment, and may increase sulphide accumulation in the sediment (Castel *et al.* 1989). Many oyster beds support encrusting macroalgae that grow on oyster shells, and abundant motile macrofauna which use oyster shells for shelter and forage on small gastropods (Griffin 1997).

Oysters and eelgrass are both found in sheltered coastal areas of relatively low wave energy. Oysters are typically found in the mid-to-high intertidal zone, while

eelgrass is constrained to the low intertidal to shallow subtidal zones. While eelgrass can be found in close proximity to oyster beds, eelgrass is typically absent directly seaward from oyster beds (Everett *et al.* 1995, pers. obs). Numerous mechanisms may contribute to the apparent exclusion of seagrass by oysters; amplification of sulphide in the sediment seaward of oyster beds is a primary concern. Oysters add large quantities of organic matter to the sediment, causing sediment conditions that favour growth of sulphide-producing bacteria (Ingold and Havill 1984, Castel *et al.* 1989, deZwaan and Babarro 2001), and high sulphide levels are associated with reduced photosynthesis and growth in eelgrass (Goodman *et al.* 1995, Holmer and Bondgaard 2001). Eelgrass transplants cannot establish in the below-oyster zone, suggesting that oysters may create an eelgrass-free below oyster zone by causing sulphide accumulation (Chapter 2). If this is the case, expansion of feral and farmed oyster beds will result in reduced eelgrass bed habitat. The first step in understanding community-level impacts of such a shift in intertidal habitat is to quantify differences in community structure between eelgrass and below-oyster habitats. The objective of this study was to compare the assemblages of fish, swimming macroinvertebrates, epibenthic macroinvertebrates and macroalgae between eelgrass bed and below-oyster habitats in order to assess the impact of replacing eelgrass beds with below-oyster zones on intertidal community structure.

METHODS

Study sites

All study sites were located on the southwest coast of Cortes Island, British Columbia, Canada (50° 4′N, 124° 56′W) (Fig 3-1). The intertidal zone directly seaward from oyster beds (the "below-oyster" zone) at the study sites was characterized by large

cobble, and was often dominated by macroalgae such as *Ulva* sp. and *Sargassum muticum* (Yendo) (pers. obs.). Below-oyster sites were located directly seaward of feral or cultured oyster beds and were at the same tidal height as adjacent eelgrass beds (Fig. 3-2). The substratum of eelgrass bed sites was characterized by a layer of mud or sand covering a layer of large cobble similar to that found in the below-oyster zone.

Epibenthic macroinvertebrates and macroalgae

Field surveys were conducted at low tide to enumerate epibenthic macroinvertebrates and macroalgae. Surveys were conducted at five eelgrass beds and four below-oyster sites (Fig 3-1). At each site, two transects (15 m) were laid perpendicular to the shoreline beginning at the low-tide line and extending through the intertidal zone onto shore. Five 0.5 m x 0.5 m quadrats were placed at random along each transect. Epibenthic macrofauna were identified to species, with the following exceptions: limpets were identified to family, and shore crabs and hermit crabs to genus. Barnacles, limpets and littorine snails, particularly in below oyster-transects, were very abundant. Thus for sampling efficiency, these taxa were enumerated as rare (0-20 individuals; exact number reported), common (21-100 individuals), abundant (101-300 individuals), or very abundant (300-1000 individuals). The exact number of individuals was recorded for all other taxa. Macroalgae were identified to species, and abundance was recorded as percent cover for each species.

Fish and swimming macroinvertebrates

Fish and swimming macroinvertebrates were sampled using a 12 m x 2 m x 1 cm mesh beach seine at eelgrass beds (N = 3 sites) and in below-oyster zones (N = 3 sites). Fish and invertebrates were identified to species and released immediately. All sets were done mid-day on an incoming tide for consistency across sampling events.

Statistical methods

T-tests were used to compare benthic macroinvertebrate abundance, macroalgal percent cover, fish species richness and abundance, and swimming macroinvertebrate species richness and abundance between eelgrass and below-oyster habitats. SPSS 11.5 software was used to perform all t-test calculations (SPSS 2002).

I analyzed assemblage structure of epibenthic organisms associated with the below-oyster zone and eelgrass beds, and fishes and swimming macroinvertebrates associated with each habitat, using the PATN software package (Belbin 1993). Eelgrass and oysters were excluded from all analyses. Category midpoints were used for epibenthic organisms for which abundance was estimated (barnacles, limpets and littorines): common = 60, abundant = 200, and very abundant = 500. Bray-Curtis distances between the quadrats were calculated based on raw, log-transformed, and presence-absence data, and semi-strong hybrid non-metric multidimensional scaling (SSH-NMDS) with 1000 random starts was used to create ordinations. SSH-NMDS was chosen as the appropriate algorithm due to its robustness to the high number of zeroes in the data matrix (Appendix 1) (Belbin 1993). Ordinations were evaluated using the PATN multivariate analysis of similarity (ANOSIM) with 1000 permutations to determine

whether assemblage structure in eelgrass beds was significantly different from that in below-oyster habitat.

Because sample size for fishes and swimming macroinvertebrates (number of seines) was inadequate for ANOSIM, Bray-Curtis distances among sites were used to create a dendrogram of fish and swimming macroinvertebrates.

RESULTS

Epibenthic macroinvertebrates and macroalgae

ANOSIM found that the assemblages of epibenthic organisms associated with eelgrass beds was significantly different from the below-oyster assemblages using raw, log-transformed, and presence-absence data ($p<0.001$ for all analyses) (Fig. 3-3).

Below-oyster transects were more species-rich than eelgrass bed transects, both in total species richness and average species richness per transect ($p=0.007$ for average species richness; Table 3-1). In total, 29 species were found in below-oyster zones compared to 22 species in eelgrass beds (Appendix 2).

Plant and macroalgal cover in eelgrass bed transects was significantly higher than in below-oyster transects ($p = 0.01$). In eelgrass bed transects, cover was dominated by *Z. marina* followed by the filamentous green alga *Enteromorpha intestinalis* and Japanese eelgrass *Z. japonica* (Table 3-2). In total, eleven plant and macroalgal species were found in eelgrass bed transects. Below-oyster transects contained a total of eight plant and macroalgal species and were dominated by *E. intestinalis* and the invasive brown alga *Sargassum muticum*.

Eleven animal taxa were found in eelgrass bed transects, while a total of twenty were found in below-oyster transects (Appendix 2). Eelgrass bed transects were

dominated by the bamboo worm *Spiochaetopterus costarum*, the dove snail *Alia carinata*, hermit crabs *Pagurus* spp., and the bubble snail *Haminoea vesicula*. Average animal abundance per below-oyster transect was significantly higher than average animal abundance per eelgrass transect ($p<0.0001$), largely due to numerical dominance of barnacles (*Balanus glandula*) in below-oyster transects (Table 3-3). In addition to barnacles, shore crabs *Hemigrapsus nudus* and *H. oregonensis*, limpets (Lottidae) and hermit crabs (*Pagurus* spp.) were common in below-oyster transects.

Fish and swimming macroinvertebrates

Eelgrass and below-oyster sets had few taxa in common (Appendix 2), as illustrated by the dendrogram (Fig 3-4) which confirms that assemblages of fish and swimming macroinvertebrates differ markedly between eelgrass and the below-oyster zones.

Eelgrass bed sites were significantly higher in overall species richness ($p = 0.006$), number of fish species ($p = 0.002$), and number of swimming macroinvertebrate species ($p = 0.02$) than below-oyster sites (Table 3-4). Abundance of fish was significantly higher in eelgrass bed seines than in below-oyster seines ($p = 0.01$), and swimming macroinvertebrates in eelgrass bed seines were slightly more abundant than in below-oyster sites ($p = 0.06$) (Table 3-5).

Representatives of eleven fish families were found in eelgrass beds. The most abundant species were the plainfin midshipman (*Porichthys notatus*, Batrachoididae), shiner perch (*Cymatogaster aggregata*, Embiotocidae) and staghorn sculpin (*Leptocottus armatus*, Cottidae). Fish abundance was significantly higher in eelgrass sets than in

below-oyster sets (p=0.002). Four fish families were found in below-oyster seines; each family was represented by a single species with the staghorn sculpin (*Leptocottus armatus*, Cottidae) being the most abundant fish present in below-oyster habitat overall.

The macroinvertebrate assemblage captured by seine in eelgrass beds consisted mainly of bubble snails (*Haminoea vesicula*), a hydrozoan jelly (*Aequoria victoria*) and kelp crabs (*Pugettia producta*) (Fig. 3-5). Abundance of macroinvertebrates was significantly higher in eelgrass beds than in below-oyster sets (t-test, p=0.02). Common species in below-oyster seines included the same hydrozoan jelly found in eelgrass beds, *A. victoria*, and a ctenophore (*Pleurobrachia bachei*) (Fig. 3-5).

DISCUSSION

Eelgrass beds and the below-oyster zone are distinct in their community structure, both in terms of epibenthic assemblages of macroinvertebrates and macroalgae (Fig 3-2), and assemblages of fish and swimming macroinvertebrates (Fig 3-3). The epibenthic assemblages in below-oyster zones displayed higher species richness and abundance than those of eelgrass beds, and the two habitats had few species in common. In contrast, fish and swimming macroinvertebrates were more abundant and their assemblages more species-rich in eelgrass beds than in below-oyster habitat.

ANOSIM confirmed that epibenthic assemblages in eelgrass and the below-oyster zone are significantly different; these differences persist even when data are transformed to reduce or eliminate the impact of high abundance of below-oyster species such as barnacles, shore crabs and limpets. This is consistent with other studies that have found assemblages associated with seagrass beds to be distinct from those associated with

unvegetated sediments (Orth and vanMontfrans 1982, Summerson and Peterson 1984, Villarreal 1995).

Many eelgrass-associated macroinvertebrates require either the soft sediment of an eelgrass bed or eelgrass blades as substrates. For example, partially buried suspension feeders (bamboo worms, *Spiochaetopterus costarum*), and gastropods that are cryptic on eelgrass blades (*Haminoea vesicula*) or roots (*Alia carinata*) were among the most common eelgrass-associated fauna. The most common below-oyster associated macroinvertebrates either required a hard surface for attachment (eg. barnacles and limpets) or preyed on small attached fauna (eg. shore crabs).

I found overall epibenthic species richness and abundance higher in the below-oyster zone than in eelgrass beds. To my knowledge, no other studies have focused on the below-oyster zone, although others have compared fauna within oyster beds to that on adjacent mudflats, sandy areas or eelgrass beds (Simenstad and Fresh 1995, Villarreal 1995, Trianni 1996, Dumbauld *et al.* 2001). Villarreal (1995) and Trianni (1996) found higher invertebrate biomass and species richness in eelgrass beds than in oyster beds and unvegetated areas; however, both of these studies included infauna as well as epibenthic species.

Simenstad and Fresh (1995) attribute the higher diversity of benthic invertebrates and macroalgae on oyster beds than on sandy areas or mudflats to increased habitat complexity created by oyster shells. Dumbauld *et al.* (2001) suggest that the increased hard surface area provided by oyster shells for attachment of macroalgae and associated invertebrates facilitates higher abundance of these organisms as compared to bare mud areas. Although the below-oyster zone is generally devoid of oyster shells, rocks provide

a similar hard surface area for attachment of barnacles, limpets and encrusting macroalgae (Fig. 3-6). In contrast, eelgrass blades and the soft, muddy substratum found in eelgrass beds are unsuitable for attachment of these organisms.

My finding that eelgrass beds possess higher fish abundance and species richness than below-oyster habitat is supported by results of other studies comparing eelgrass bed fauna to that of nearby unvegetated sediments (Orth *et al.* 1984, Summerson and Peterson 1984, Lubbers *et al.* 1990, Mattila *et al.* 1999, Manderson *et al.* 2000, Murphy *et al.* 2000). Several experimental studies have found significantly lower predation on fish in seagrass beds than in unvegetated areas (Rooker *et al.* 1998, Manderson *et al.* 2000, Linehan *et al.* 2001). The complex physical structure of an eelgrass bed provides protection from predation for fish as well as for swimming and epifaunal macroinvertebrates (Heck and Orth 1980, Orth *et al.* 1984, Summerson and Peterson 1984, Lubbers *et al.* 1990, Sogard and Able 1991, Connolly 1994, Rooker *et al.* 1998, Murphy *et al.* 2000, Sheridan and Minello 2003).

Differences in availability of food for fish and swimming macroinvertebrates in eelgrass beds as compared to unvegetated areas may also be a contributing factor in the higher abundance of swimming organisms in eelgrass bed seines (Marsh 1973, Orth and vanMontfrans 1982, Lubbers *et al.* 1990, Connolly 1994). Slower water currents above eelgrass beds trap plankton and detritus in the water column, making them available to eelgrass bed inhabitants including juvenile fishes and suspension-feeding epifauna (Summerson and Peterson 1984, Lubbers *et al.* 1990, Jones *et al.* 1994). Eelgrass leaves provide substantial surface area for attachment of epiphytic algae and small grazers,

which are important sources of food for kelp crabs and juvenile fishes (Hines 1982, Lubbers *et al.* 1990).

Both native eelgrass and non-native oysters act as ecosystem engineers by altering the physical conditions of their habitat and thereby controlling resource availability for other organisms (Coleman and Williams 2002). Associated with each of these engineer species is a distinct community structure; linked to the presence of oysters is the below-oyster zone and its characteristic assemblages of fish, macroinvertebrates and macroalgae. Because the current distributions of oyster beds and eelgrass suggest that substantial sections of eelgrass beds have been replaced with below-oyster habitat, it is likely that extensive regions of coastal Cortes Island have undergone alterations in abundance and diversity of macroalgae, invertebrates and fish. The results of this study reinforce the importance of eelgrass conservation in coastal British Columbia. Although further research is required to determine whether a causal link exists between oyster bed establishment and eelgrass beds being replaced by below-oyster habitat, further expansion of ground-culture oyster farms should be limited to areas well away from eelgrass beds.

TABLES AND FIGURES

Table 3-1. Epibenthic macroinvertebrate and macroalgae species richness (N = 30 transects in 5 eelgrass beds, 24 transects in 4 below-oyster zone sites)

Habitat	Total species richness	Average species richness per transect (N = 5 quadrats/transect)	SE
Eelgrass			
Overall	22	7.5	0.45
Plants, macroalgae	11	3.5	0.31
Macroinvertebrates	11	4.0	0.23
Below-oyster			
Overall	29	9.1	0.43
Plants, macroalgae	9	3.6	0.28
Macroinvertebrates	20	5.5	0.39

Table 3-2. Percent cover of plants and epibenthic macroalgae in eelgrass and below-oyster transects (N = 30 transects in 5 eelgrass beds, 24 transects in 4 below-oyster zone sites; 5 quadrats per transect)

	Average percent cover	SE
Eelgrass – 11 plant species		
Plants and macroalgae	68	3.12
Z. marina	50.3	3.19
E. intestinalis	8.1	2.22
Z. japonica	6.1	2.67
Below-oyster – 8 plant species		
Plants and macroalgae	50.3	7.69
E. intestinalis	33.5	6.97
S. muticum	11.9	4.04

Table 3-3. Most abundant macroinvertebrate taxa in eelgrass and below-oyster transects (N = 30 transects in 5 eelgrass beds, 24 transects in 4 below-oyster zone sites)

	Average number of individuals per transect (N = 5 quadrats/transect)	SE
Eelgrass		
All macroinvertebrates	57.3	5.39
Bamboo worm (*Spiochaetopterus costarum*)	24.6	3.25
Dove snail (*Alia carinata*)	23.7	5.18
Hermit crabs (*Pagurus* sp.)	4.9	1.06
Bubble snail (*Haminoea vesicula*)	1.7	0.77
Below-oyster		
* All macroinvertebrates	801.5	80.75
* Barnacles (*Balanus glandula*)	730.0	73.99
Shore crabs (*Hemigrapsus* sp.)	23.5	6.01
* Limpets (Fam. Lottidae)		
Hermit crabs (*Pagurus* sp.)	9.71	3.32

* average based on estimated abundance for barnacles, limpets and/or littorine snails

Table 3-4. Fish and swimming macroinvertebrate species richness (N = 3 seines/habitat)

	Total species richness	Average species richness per seine	SE
Eelgrass			
Overall	36	23.0	2.89
Fish	22	13.0	1.15
Invertebrates	14	10.0	1.73
Below-oyster			
Overall	11	6.00	2.52
Fish	5	2.33	1.33
Invertebrates	6	3.67	1.20

Table 3-5. Most abundant fish and swimming macroinvertebrate species in seines (N = 3 seines/habitat)

	Average number of individuals per seine	SE
Eelgrass		
All animals	663.7	161.38
All fishes – 11 families	317.3	81.34
Plainfin midshipman (*Porichthys notatus*)	102.5	67.36
Shiner perch (*Cymatogaster aggregata*)	89.0	17.15
Staghorn sculpin (*Leptocottus armatus*)	85.0	40.86
All swimming macroinvertebrates	346.3	155.30
Bubble snails (*Haminoea vesicula*)	175.0	140.34
Hydrozoan jelly (*Aequoria victoria*)	70.7	44.80
Kelp crab (*Pugettia producta*)	31.0	15.31
Below-oyster		
All animals	48.0	17.78
All fishes – 4 families	11.3	5.24
Staghorn sculpin (*Leptocottus armatus*)	8.3	2.73
All swimming macroinvertebrates	36.7	16.33
Hydrozoan jelly (*Aequoria victoria*)	29.5	3.67
Comb jelly (*Pleurobrachia bachei*)	14.0	6.56

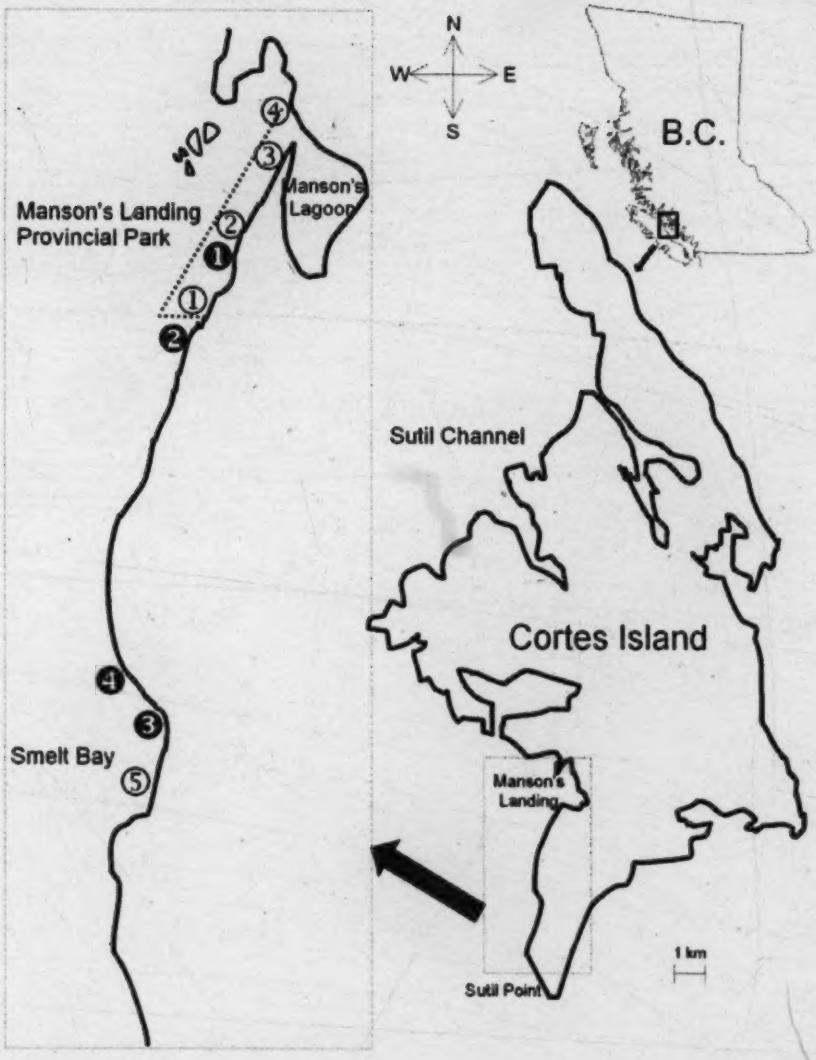

Figure 3-1. Map of Cortes Island with detail of study sites. Unfilled circles indicate eelgrass bed sites; filled circles indicate below-oyster sites. Sites BO-1 and 3 were below feral oyster beds, while sites BO-2 and 4 were located below cultured oyster beds. Sites were classified as eelgrass (EEL) or below-oyster (BO). Sampling sites EEL-1, 2, 3 and 4, and BO-1 were located in Manson's Landing Provincial Park, and BO-2 was immediately south of the park; sites EEL-5 and BO-3 and 4 were located directly north of Smelt Bay Provincial Park (Fig. 1).

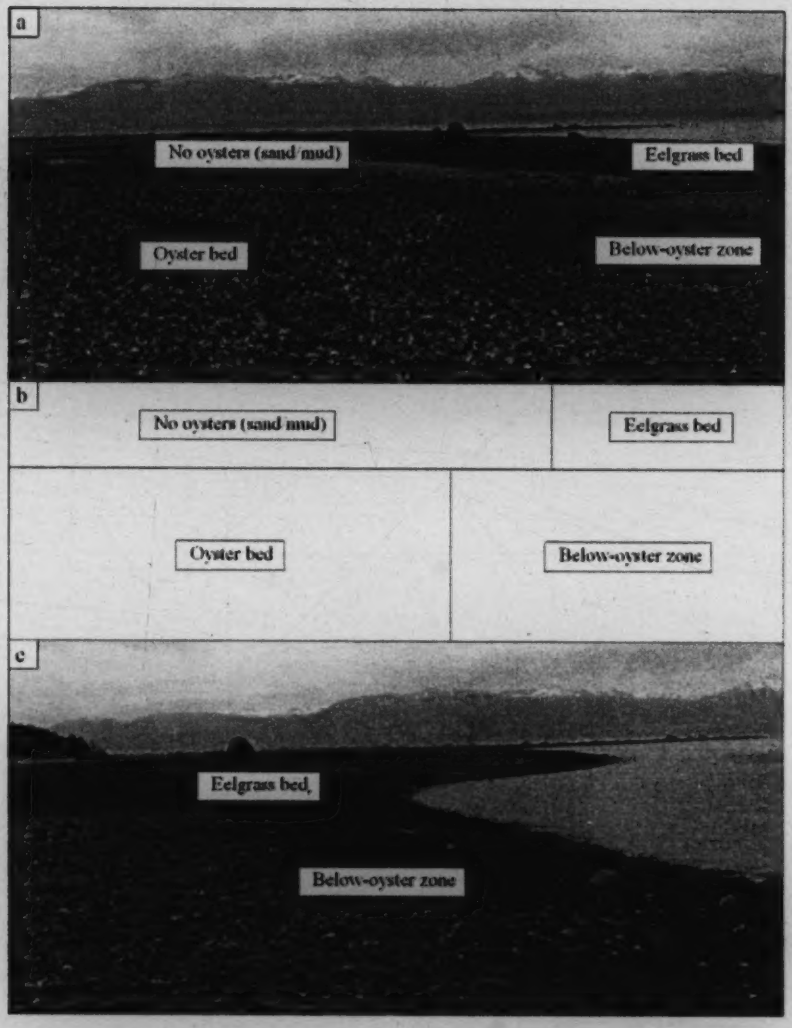

Figure 3-2. Study site layout. (a) shows physical relationship of below-oyster zone to oyster bed and eelgrass bed. (b) shows schematic diagram of below-oyster zone, oyster bed and eelgrass bed. (c) shows below-oyster zone and adjacent eelgrass bed.

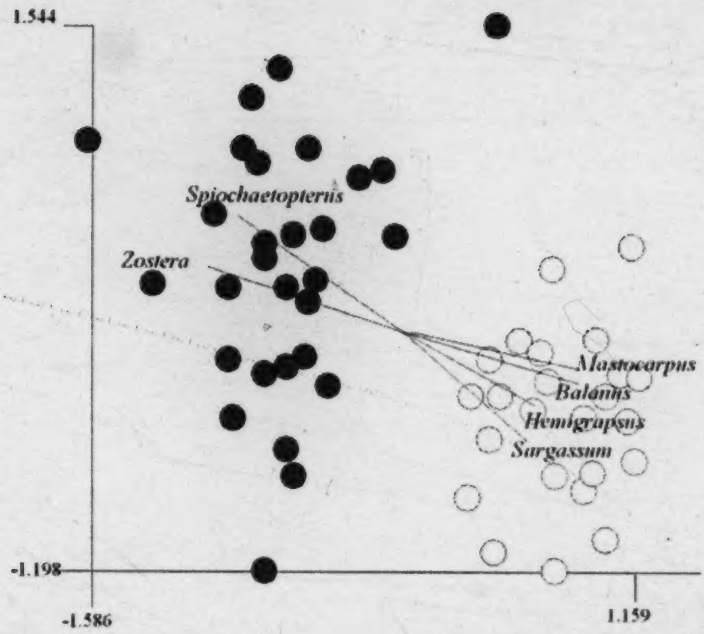

Figure 3-3. Two-dimensional ordination created using SSH-NMDS (semi-strong hybrid non-metric multidimensional scaling) with 1000 random starts in PATN software. Filled circles represent eelgrass bed transects (n = 30); unfilled circles represent below-oyster transects (n = 24). NMDS stress = 0.1227. ANOSIM $p < 0.001$. Vectors represent maximum correlation between each taxon and samples; all vectors shown are significant ($p<0.05$).

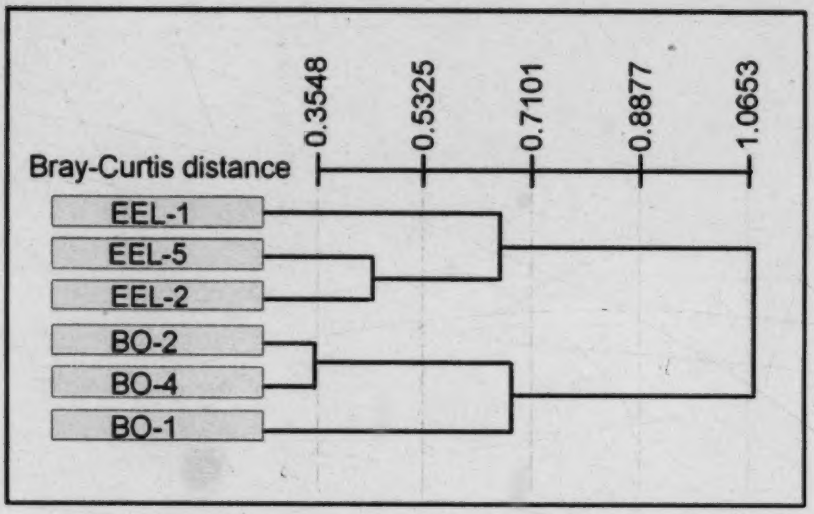

Figure 3-4. Dendrogram of fish and swimming macroinvertebrate assemblages in eelgrass and below-oyster habitats. Bray-Curtis association measure was used to determine multivariate distances between sites. Site numbers correspond to Fig. 3-1.

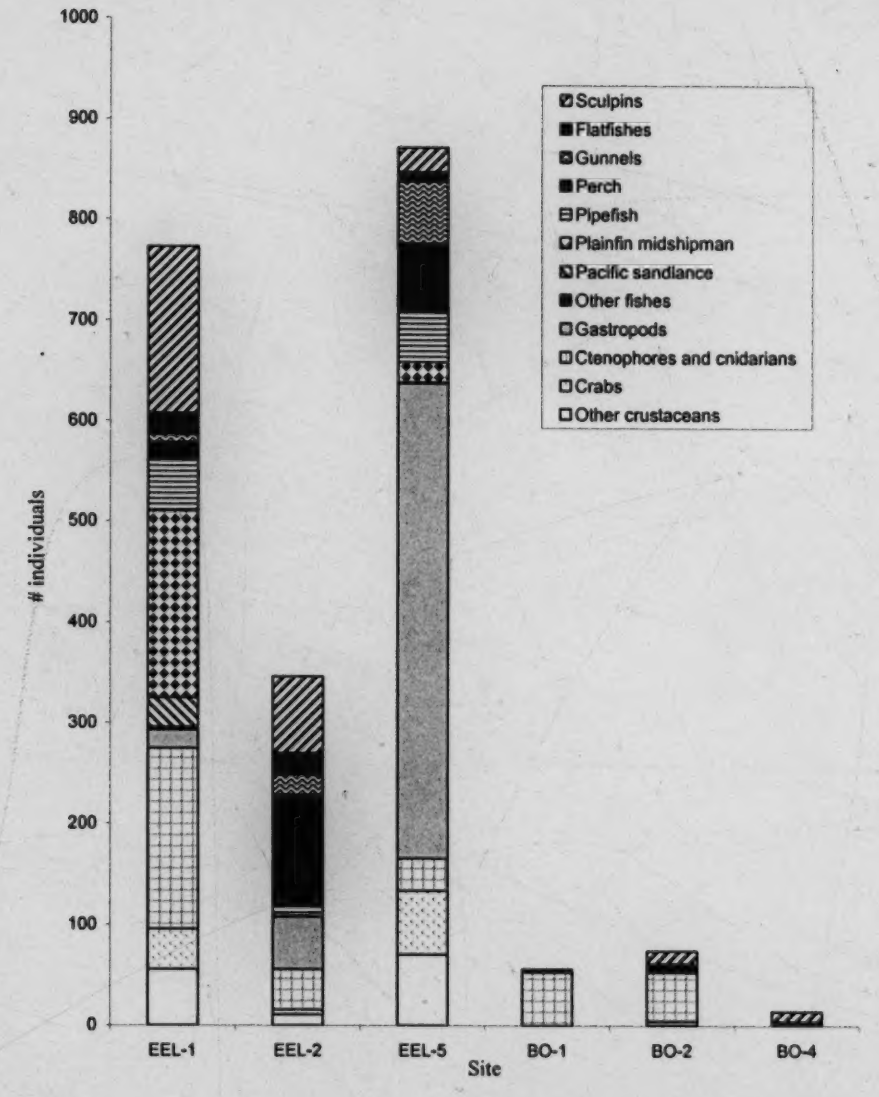

Figure 3-5. Fish and swimming macroinvertebrates caught in seines at eelgrass bed and below-oyster sites. Each bar represents one seine haul.

Figure 3-6. Examples of below-oyster zone habitat (a, b) and eelgrass bed habitat (c,d) at same intertidal height. Green macroalgae pictured in (a) and (b) is *E. intestinalis*.

REFERENCES

BCSGA. 2003. Information resource centre. BC Shellfish Growers Association http://www.bcsga.ca. Accessed 21 Feb 2005.

Belbin, L. 1993. PATN (Pattern Analysis Package) Technical Reference. Australia: CSIRO.

Castel, J., J-P. Labourg, V. Escaravage, I. Auby, and M.E. Garcia. 1989. Influence of seagreass beds and oyster parks on the abundance and biomass patterns of meio- and macrobenthos in tidal flats. Estuarine, Coastal and Shelf Science **28**:71-85.

Coleman, F. C., and S.L. Williams. 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends in Ecology and Evolution **17**:40-44.

Connolly, R. M. 1994. The role of seagrass as preferred habitat for juvenile *Sillaginodes punctata* (Cuv. & Val.) (Sillaginidae, Pisces): habitat selection or feeding? Journal of Experimental Marine Biology and Ecology **180**:39-47.

deZwaan, A., and J.M.F. Babarro. 2001. Studies on the causes of mortality of the estuarine bivalve *Macoma balthica* under conditions of (near) anoxia. Marine Biology **138**:1021-1028.

Dumbauld, B., K.M. Brooks, and M.H. Posey. 2001. Response of an estuarine benthic community to application of the pesticide carbaryl and cultivation of Pacific oysters (*Crassostrea gigas*) in Willapa Bay, Washington. Marine Pollution Bulletin **42**:826-844.

Everett, R., G.M. Ruiz, and J.T. Carlton. 1995. Effect of oyster mariculture on submerged aquatic vegetation - an experimental test in a Pacific Northwest estuary. Marine Ecology Progress Series **125**:205-217.

Goodman, J. L., K.A. Moore and W.C. Dennison. 1995. Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon. Aquatic Botany **50**:37-47.

Griffin, K. 1997. Eelgrass ecology and commercial oyster cultivation in Tillamook Bay, Oregon. Tillamook Bay National Estuary Project Report #11-97.

Heck, K. L., and R.J. Orth. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. Pages 449-464 in V. S. Kennedy, editor. Estuarine perspectives. Academic Press, New York.

Hines, A. H. 1982. Coexistence in a kelp forest: size, population dynamics, and resource partitioning in a guild of spider crabs (Brachyura, Majidae). Ecological Monographs **52**:179-198.

Holmer, M., and E. J. Bondgaard. 2001. Photosynthetic and growth response of eelgrass to low oxygen and high sulfide concentrations during hypoxic events. Aquatic Botany **70**:29-38.

Ingold, A., and D.C. Havill. 1984. The influence of sulphide on the distribution of higher plants in salt marshes. Journal of Ecology **72**:1043-1054.

Jones, C. G., J.H. Lawton and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos **69**:373-386.

Jones, C. G., J.H. Lawton and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology **78**:1946-1957.

Linehan, J. E., R.S. Gregory, and D.C. Schneider. 2001. Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. Journal of Experimental Marine Biology and Ecology **263**:25-44.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8**:133-137.

Loreto, M. L., M. Lara and J.J. Schmitter-Soto. 2003. Coral reef fish assemblages at Banco Chinchorro, Mexican Caribbean. Bulletin of Marine Science **73**:153-170.

Lubbers, L., W.R. Boynton, and W.M. Kemp. 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. Marine Ecology Progress Series **65**:1-14.

Manderson, J. P., B.A. Phelan, and A.W. Stoner. 2000. Predator-prey relations between age-1+ summer flounder (Paralichthys dentatus L.) and age-0 winter flounder (Pseudopleuronectes americanus Walbaum): predator diets, prety selection and effects of sediments and macrophytes. Journal of Experimental Marine Biology and Ecology **251**:17-39.

Marsh, G. A. 1973. The Zostera epifaunal community in the York River, Virginia. Chesapeake Science **14**:87-97.

Mattila, J., G. Chaplin, M.R. Eilers, K.L. Heck, J.P. O'Neal, and J.F. Valentine. 1999. Spatial and diurnal distribution of invertebrate and fish fauna of a *Zostera marina* bed and nearby unvegetated sediments in Damariscotta River, Maine (USA). Journal of Sea Research **41**:321-332.

Mumby, P. J., A. J. Edwards, J. E. Arias-Gonzalez, K.C. Lindeman, P.G. Blackwell, A. Gall, M.L. Gorczynska, A. R. Harborne, C.L. Pescod, H. Renken, C. C. C. Wabnitz, and G. Llewellyn. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature **427**:533-536.

Murphy, M. L., S.W. Johnson, and D.J. Csepp. 2000. A comparison of fish assemblages in eelgrass and adjacent subtidal habitats near Craig, Alaska. Alaska Fishery Research Bulletin **7**:11-21.

Orth, R., and J. vanMontfrans. 1982. Structural analysis of benthic communities associated with vegetated and unvegetated habitats. Pages 232 pp. in R. J. Orth, and J. vanMontfrans, editor. Interactions of Resident Consumers in a Temperate Estuarine Seagrass Community: Vaucluse Shores, Virginia, USA. Virginia Institute of Marine Sciences.

Orth, R., K.L. Heck, and J. Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries **7**:339-350.

Quayle, D. 1964. Distribution of introduced marine mollusca in British Columbia waters. Journal of the Fisheries Research Board of Canada **21**:1155-1164.

Reise, K. 1985. Tidal Flat Ecology. Springer-Verlag, Berlin. 191 pp.

Reise, K., E. Herre and M. Sturm. 1989. Historical changes in the benthos of the Wadden Sea around the island of Sylt in the North Sea. Helgoländer Meeresuntersuchungen **43**:413-433.

Rooker, J. R., G.J. Holt, and S.A. Holt. 1998. Vulnerability of newly settled red drum (*Sciaenops ocellatus*) to predatory fish: is early-life survival enhanced by seagrass meadows? Marine Biology **131**:145-151.

Sheridan, P., and T.J. Minello. 2003. Nekton use of different habitat types in seagrass beds of Lower Laguna Madre, Texas. Bulletin of Marine Science **72**:37-61.

Simenstad, C., and K.I. Fresh. 1995. Influence of intertidal aquaculture on benthic communities in Pacific Northwest estuaries: scales of disturbance. Estuaries **18**:43-70.

Sogard, S. M., and K.W. Able. 1991. A comparision of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. Estuarine, Coastal and Shelf Science **33**:501-519.

Summerson, H. C., and C.H. Peterson. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. Marine Ecology Progress Series **15**:63-77.

Trianni, M. S. 1996. The influence of commercial oyster culture activities on the benthic infauna of Arcata Bay. Humboldt State University, Humboldt, CA.

Villarreal, G. 1995. Alterations in the structure of the macrobenthic community at Bahia Falsa, Mexico, related to the culture of Crassostrea gigas. Ciencias Marinas **21**:373-386.

Wyllie-Echeverria, S., T. Mumford, J. Gaydos and S. Buffum. 2003. *Z. marina* declines in San Juan County, WA. Westcott Bay Taskforce Mini-Workshop.

SUMMARY AND CONCLUSIONS

I investigated the indirect effects of the introduced Pacific oyster (*Crassostrea gigas* Thunberg) on eelgrass health and intertidal community structure on Cortes Island, British Columbia, Canada. Oysters physically alter their new environment by increasing habitat complexity and altering water flow (Coleman and Williams 2002), and possibly by causing sulphide to accumulate in the sediment (Dahlback and Gunnarsson 1981, Castel *et al.* 1989, Grant *et al.* 1995, Nugues 1996, Sorokin *et al.* 1999). Sulphide is toxic to native eelgrass (*Zostera marina* L.) (Goodman *et al.* 1995, Holmer and Bondgaard 2001), and the current decline of native eelgrass in this region may be a consequence of feral oyster population growth (Fig 4-1). While oysters and eelgrass coexist at a regional scale, eelgrass is typically absent directly seaward of oyster beds (the "below-oyster zone") on Cortes Island (pers. obs.).

I compared nektonic (fish and swimming macroinvertebrates) and epibenthic (macroinvertebrates and macroalgae) assemblages between eelgrass bed and below-oyster habitats to assess impacts of the shift from eelgrass to below-oyster habitat. I sampled the intertidal zone on Cortes Island at low tide using two methods: quadrats to enumerate epibenthic macroinvertebrates and macroalgae, beach seines to enumerate fish and swimming macroinvertebrates. Using multivariate analyses of similarity (ANOSIM), I found that the structure of eelgrass-bed nektonic and epibenthic assemblages were significantly different from those associated with below-oyster zones. Nektonic species richness and abundance were higher in eelgrass beds than in below-oyster habitat (t-test, $p = 0.006$ and $p = 0.01$, respectively). These results are supported by other studies that have found higher fish species richness and abundance in eelgrass beds than on nearby

unvegetated sediments, although other studies have not focused specifically on the below-oyster zone (Orth *et al.* 1984, Summerson and Peterson 1984, Lubbers *et al.* 1990, Mattila *et al.* 1999, Manderson *et al.* 2000). Epibenthic species richness and abundance were significantly higher in below-oyster habitat than in eelgrass beds (t-test, $p = 0.007$ and $p = 0.01$, respectively). To my knowledge, this is the first study to compare epibenthic assemblages of the below-oyster zone to those of eelgrass beds.

Because a common method of eelgrass-bed rehabilitation involves transplanting, I transplanted plugs of *Z. marina* to below-oyster plots to determine whether this habitat is suitable for eelgrass growth. I also transplanted plugs into eelgrass beds to control for effects of the transplanting process. Number of leaves present initially declined in all cores after transplanting, but only those transplanted within eelgrass beds had recovered by the end of the experiment. Shoot and leaf number were significantly greater over time in eelgrass-bed transplants than in below-oyster transplants (repeated-measures ANOVA $p<0.05$). These results indicate that the below-oyster zone is unsuitable for eelgrass growth; this may be due to sulphide toxicity as sediment sulphide levels below oyster beds were 6 times higher than sediment sulphide in eelgrass beds.

If a causal link exists between oyster presence in the high intertidal zone and eelgrass absence directly seaward, then expansion of feral and farmed oyster beds will result in further eelgrass loss. This change from eelgrass bed to below-oyster habitat in the low intertidal zone will result in a dramatic shift in intertidal community structure, likely including a reduction in fish diversity and abundance, and an increase in small gastropods and crustaceans such as littorine snails, barnacles and shore crabs.

These results have direct implications for management and conservation of eelgrass beds. As natural re-establishment is rare once eelgrass has been lost from an area, transplants are generally the only option for restoration (Peralta *et al.* 2003). Transplants have been used to expand and re-establish eelgrass meadows around the world (Homziak *et al.* 1982, Harrison 1987, 1990, Phillips 1990, deJonge *et al.* 1996). The goal of such transplanting projects is to establish vegetation so that the diverse community associated with eelgrass beds can develop (Homziak *et al.* 1982). Previous studies have shown that restoration success depends on the cause of eelgrass loss as well as the degree of environmental change following eelgrass loss (Harrison 1990, deJonge *et al.* 1996. Reusch and Williams 1998, Peralta *et al.* 2003).

The results of this study underscore the importance of eelgrass conservation for maintaining intertidal community structure, and demonstrate that simple transplanting will likely be ineffective for mitigation of eelgrass loss below oyster beds on Cortes Island. Research should focus on investigating a more effective means of eelgrass restoration in these areas; for example, before transplanting is attempted in below-oyster zones it may be necessary to remove oysters and allow time for the site to return to pre-oyster sediment conditions. The British Columbia Shellfish Growers' Association (2003) states that industry growth will focus on increasing productivity of current shellfish aquaculture sites rather than expanding production areas. The results of my study suggest that this may be the most eelgrass-safe route to increasing oyster aquaculture, and that any new beach-culture leases should be issued only in areas well away from eelgrass beds to prevent further losses of eelgrass below oysters. However, the British Columbia Ministry of Sustainable Resource Management has indicated that applications for new

beach-culture leases will be considered in all eight planning units on and around Cortes Island, including seven planning units identified as containing eelgrass beds (Truscott *et al.* 2005). In these planning units, shellfish farmers are instructed to "implement measures" to avoid negative impacts to eelgrass when leases are directly adjacent to eelgrass beds (Truscott *et al.* 2005). Development of such measures to mitigate impacts of shellfish farming on eelgrass beds will be an important area for future research. One such measure might include the culture of triploid oysters in order to prevent spawning and subsequent expansion of feral oyster populations. Eelgrass protection and restoration efforts are necessary for conservation of the distinct assemblages associated with eelgrass, and as such must be addressed in management and coastal development planning.

FIGURES

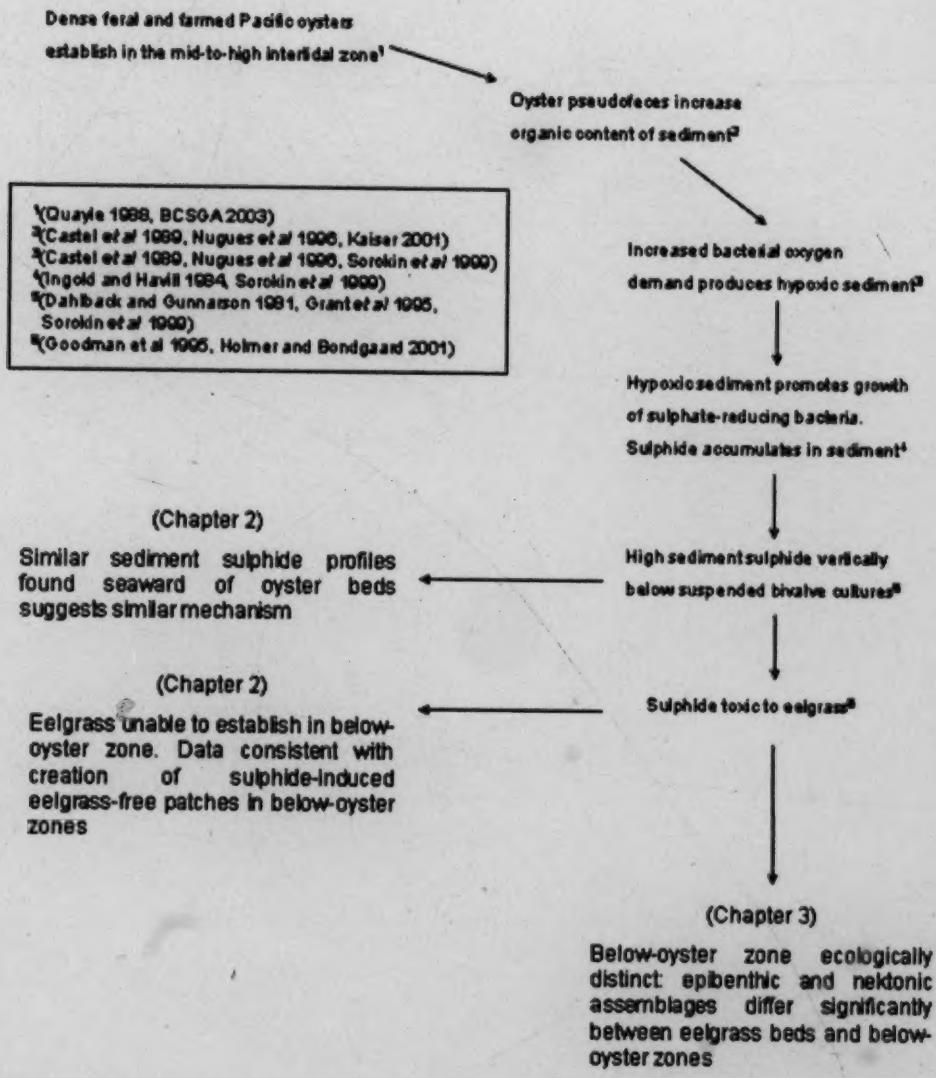
Dense feral and farmed Pacific oysters establish in the mid-to-high intertidal zone[1]
Oyster pseudofeces increase organic content of sediment[2]
[1](Quayle 1988, BCSOA 2003)
[2](Castel et al 1989, Nugues et al 1996, Kaiser 2001)
[3](Castel et al 1989, Nugues et al 1996, Sorokin et al 1999)
[4](Ingold and Havill 1984, Sorokin et al 1999)
[5](Dahlback and Gunnarson 1981, Grant et al 1995, Sorokin et al 1999)
[6](Goodman et al 1995, Holmer and Bondgaard 2001)
Increased bacterial oxygen demand produces hypoxic sediment[3]
Hypoxic sediment promotes growth of sulphate-reducing bacteria. Sulphide accumulates in sediment[4]
High sediment sulphide vertically below suspended bivalve cultures[5]
(Chapter 2)
Similar sediment sulphide profiles found seaward of oyster beds suggests similar mechanism
Sulphide toxic to eelgrass[6]
(Chapter 2)
Eelgrass unable to establish in below-oyster zone. Data consistent with creation of sulphide-induced eelgrass-free patches in below-oyster zones
(Chapter 3)
Below-oyster zone ecologically distinct: epibenthic and nektonic assemblages differ significantly between eelgrass beds and below-oyster zones

Figure 4-1. Schematic diagram of eelgrass-oyster interactions on Cortes Island based on literature and thesis research results.

REFERENCES

BCSGA. 2003. Information resource centre. BC Shellfish Growers Association http://www.bcsga.ca. Accessed 21 Feb 2005.

Castel, J., J-P. Labourg, V. Escaravage, I. Auby, and M.E. Garcia. 1989. Influence of seagreass beds and oyster parks on the abundance and biomass patterns of meio- and macrobenthos in tidal flats. Estuarine, Coastal and Shelf Science **28**:71-85.

Coleman, F. C., and S.L. Williams. 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends in Ecology and Evolution **17**:40-44.

Dahlback, B., and L.A.H. Gunnarsson. 1981. Sedimentation and sulfate reduction under a mussel culture. Marine Biology **63**:269-275.

deJonge, V. N., deJong, D.J., and van den Bergs, J. 1996. Reintroduction of eelgrass (*Zostera marina*) in the Dutch Wadden Sea; review of research and suggestions for management measures. Journal of Coastal Conservation **2:** 149-158.

Goodman, J. L., K.A. Moore and W.C. Dennison. 1995. Photosynthetic responses of eelgrass (*Zostera marina* L.) to light and sediment sulfide in a shallow barrier island lagoon. Aquatic Botany **50**:37-47.

Grant, J., A. Hatcher, D.B. Scott, P. Pocklington, C.T. Shafer, and G.V. Winters. 1995. A multidisciplinary approach to evaluating impacts of shellfish aquaculture on benthic communities. Estuaries **18**:124-144.

Harrison, P. G. 1987. Natural expansion and experimental manipulation of seagrass (*Zostera* spp.) abundance and the response of infaunal invertebrates. Estuarine, Coastal and Shelf Science **24**:799-812.

Harrison, P. G. 1990. Variations in success of eelgrass transplants over a five-years' period. Environmental Conservation **17**:157-163.

Holmer, M., and E. J. Bondgaard. 2001. Photosynthetic and growth response of eelgrass to low oxygen and high sulfide concentrations during hypoxic events. Aquatic Botany **70**:29-38.

Homziak, J., M.S. Fonseca and W.J. Kenworthy. 1982. Macrobenthic community structure in a transplanted eelgrass (*Zostera marina*) meadow. Marine Ecology Progress Series **9**:211-221.

Kaiser, M. J. 2001. Ecological effects of shellfish cultivation. Pages 51-75 *in* K. D. Black, editor. Environmental Impacts of Aquaculture. Sheffield Academic Press, Sheffield, UK.

Lubbers, L., W.R. Boynton, and W.M. Kemp. 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. Marine Ecology Progress Series **65**:1-14.

Manderson, J. P., B.A. Phelan, and A.W. Stoner. 2000. Predator-prey relations between age-1+ summer flounder (*Paralichthys dentatus* L.) and age-0 winter flounder (*Pseudopleuronectes americanus* Walbaum): predator diets, prey selection and effects of sediments and macrophytes. Journal of Experimental Marine Biology and Ecology **251**:17-39.

Mattila, J., G. Chaplin, M.R. Eilers, K.L. Heck, J.P. O'Neal, and J.F. Valentine. 1999. Spatial and diurnal distribution of invertebrate and fish fauna of a *Zostera marina* bed and nearby unvegetated sediments in Damariscotta River, Maine (USA). Journal of Sea Research **41**:321-332.

Nugues, M. 1996. Benthic community changes associated with intertidal oyster cultivation. Aquaculture Research **27**:913-924.

Orth, R., K.L. Heck, and J. Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries **7**:339-350.

Peralta, G., T.J. Bouma, J. vanSoelen, J.L. Perez-Llorens, and I. Hernandez. 2003. On the use of sediment fertilization for seagrass restoration: a mesocosm study on *Zostera marina* L. Aquatic Botany **75**:95-110.

Phillips, R. C. 1990. Transplant methods. Pages 51-54 *in* R. C. Phillips, and C.P. McRoy, editor. Seagrass research methods. UNESCO, Paris, France.

Quayle, D. 1988. Pacific oyster culture in British Columbia. Canadian Bulletin of Fisheries and Aquatic Sciences **218**:241 p.

Reusch, T. B. H., and S.L. Williams. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. Oecologia **113**:428-441.

Sorokin, I. I., O. Giovanardi, F. Pranovi and P.I. Sorokin. 1999. Need for restricting bivalve culture in the southern basin of the Lagoon of Venice. Hydrobiologia **400**:141-148.

Summerson, H. C., and C.H. Peterson. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. Marine Ecology Progress Series **15**:63-77.

Truscott, J., J. Bones, C. Egan, G. Winterbottom and R. Paynter. 2005. Cortes Island Coastal Report for Shellfish Aquaculture. British Columbia Ministry of Sustainable Resource Management, Coast & Marine Planning Branch.

Appendix 1. Field survey data. Plant and macroalgal cover are indicated as average percent cover from 5 quadrats along each transect. Animal abundance is indicated as total count per transect or per seine haul.

		Eelgrass - Site 1					
		June		July		August	
Genus	Species	Transect 1	Transect 2	Transect 1	Transect 2	Transect 1	Transect 2
Zostera	*japonica*	0%	0%	0%	0%	0%	0%
Zostera	*marina*	45%	36%	60%	76%	47%	29%
Fucus	*gardneri*	0%	0%	0%	0%	0%	0%
Leathesia	*difformis*	0%	0%	0%	0%	0%	0%
Sargassum	*muticum*	0%	0%	0%	0%	0%	0%
Calliarthron	*tuberculosum*	0%	0%	0%	0%	0%	0%
Ceramium	*californicum*	0%	0%	3%	4%	0%	0%
Chondracanthus	*exasperatus*	0%	0%	0%	0%	0%	0%
Gracilaria	cf. *pacifica*	0%	0%	0%	0%	0%	0%
Mastocarpus	*papillatus*	0%	0%	0%	0%	0%	0%
Enteromorpha	*intestinalis*	6%	7%	5%	11%	0%	0%
Ulva	cf. *fenestrata*	0%	0%	0%	0%	0%	1%
Anthopleura	*elegantissima*	0	0	0	0	0	0
Aequorea	*victoria*	0	0	0	0	0	0
Aurelia	*aurita*	0	0	0	0	0	0
Pleurobrachia	*bachei*	0	0	0	0	0	0
Heptacarpus	*sitchensis*	0	0	0	0	0	0
Crangon	sp.	0	0	0	0	0	0
Pandalus	*danae*	0	0	0	0	0	0
Ligia	*pallasii*	0	0	0	0	0	0
Balanus	*glandula*	0	0	0	0	0	0
Hemigrapsus	spp.	0	0	2	2	3	2
Cancer	*magister*	0	0	0	0	0	0
Pagurus	spp.	2	0	5	4	19	7
Oregonia	*gracilis*	0	0	0	0	0	0
Pugettia	*producta*	0	0	1	0	0	1
Petrolisthes	*cinctipes*	0	0	0	0	0	0
Spiochaetopterus	*costarum*	29	25	29	30	36	38
Eudistylia	*vancouveri*	0	1	0	0	0	0
Alia	*carinata*	0	0	9	17	23	7
Amphissa	*versicolor*	0	0	0	1	0	0
Littorina	*spp.*	0	0	0	0	0	0
Batillaria	*zonalis*	0	0	0	0	0	0
Nucella	*lamellosa*	0	0	0	0	0	0
Archidoris	*montereyensis*	0	0	0	0	0	0
Haminoea	*virescens*	0	0	0	0	0	0
Mopalia	*muscosa*	0	0	0	0	0	0
Mytlius	*trossulus*	0	0	0	0	0	0
Lottia and *Tectura*	spp.	0	0	0	0	0	0
Amphipholis	cf. *squamata*	0	0	0	0	0	0
Pisaster	*ochraceus*	0	0	0	0	0	0
Pycnopodia	*helianthoides*	0	0	0	0	0	0
Dendraster	*excentricus*	0	0	0	0	0	0
Cnemidocarpa	*finmarkiensis*	0	0	0	0	0	0

Genus	Species	Eelgrass - Site 2					
		June		July		August	
		Transect 1	Transect 2	Transect 1	Transect 2	Transect 1	Transect 2
Zostera	*japonica*	0%	0%	19%	0%	44%	51%
Zostera	*marina*	59%	44%	60%	90%	22%	31%
Fucus	*gardneri*	0%	0%	0%	0%	0%	0%
Leathesia	*difformis*	0%	0%	0%	0%	0%	0%
Sargassum	*muticum*	0%	0%	0%	0%	0%	0%
Calliarthron	*tuberculosum*	0%	0%	0%	0%	0%	0%
Ceramium	*californicum*	0%	0%	0%	0%	0%	0%
Chondracanthus	*exasperatus*	0%	0%	0%	0%	0%	0%
Gracilaria	*cf. pacifica*	0%	0%	0%	0%	0%	0%
Mastocarpus	*papillatus*	0%	0%	0%	0%	0%	0%
Enteromorpha	*intestinalis*	0%	2%	5%	0%	0%	0%
Ulva	*cf. fenestrata*	1%	0%	0%	0%	0%	0%
Anthopleura	*elegantissima*	0	0	0	0	0	0
Aequorea	*victoria*	0	0	0	0	0	0
Aurelia	*aurita*	0	0	0	0	0	0
Pleurobrachia	*bachei*	0	0	0	0	0	0
Heptacarpus	*sitchensis*	0	0	0	0	0	0
Crangon	*sp.*	0	0	0	0	0	0
Pandalus	*danae*	0	0	0	0	0	0
Ligia	*pallasii*	0	0	0	0	0	0
Balanus	*glandula*	0	0	0	0	0	0
Hemigrapsus	*spp.*	5	3	1	2	2	3
Cancer	*magister*	0	0	0	0	0	0
Pagurus	*spp.*	0	0	8	22	8	17
Oregonia	*gracilis*	0	0	0	0	0	0
Pugettia	*producta*	0	0	0	0	0	0
Petrolisthes	*cinctipes*	0	0	0	0	0	0
Spiochaetopterus	*costarum*	50	0	48	42	63	54
Eudistylia	*vancouveri*	0	0	0	0	0	0
Alia	*carinata*	0	0	25	15	0	10
Amphissa	*versicolor*	0	0	0	0	0	0
Littorina	*spp.*	0	0	0	0	0	0
Batillaria	*zonalis*	0	0	0	0	0	0
Nucella	*lamellosa*	0	0	0	0	0	0
Archidoris	*montereyensis*	0	0	0	0	0	0
Haminoea	*virescens*	0	0	0	0	0	0
Mopalia	*muscosa*	0	0	0	0	0	0
Mytlius	*trossulus*	0	0	0	0	0	0
Lottia and *Tectura*	*spp.*	0	0	0	0	0	0
Amphipholis	*cf. squamata*	0	0	0	0	0	0
Pisaster	*ochraceus*	0	0	0	0	0	0
Pycnopodia	*helianthoides*	0	0	0	0	0	0
Dendraster	*excentricus*	0	0	0	0	0	0
Cnemidocarpa	*finmarkiensis*	0	0	0	0	0	0

Eelgrass - Site 3

Genus	Species	June Transect 1	June Transect 2	July Transect 1	July Transect 2	August Transect 1	August Transect 2
Zostera	*japonica*	0%	0%	0%	0%	0%	0%
Zostera	*marina*	45%	25%	27%	35%	69%	59%
Fucus	*gardneri*	0%	0%	0%	0%	0%	0%
Leathesia	*difformis*	0%	0%	1%	1%	0%	0%
Sargassum	*muticum*	0%	0%	3%	0%	0%	0%
Calliarthron	*tuberculosum*	0%	0%	2%	2%	0%	0%
Ceramium	*californicum*	0%	0%	0%	0%	0%	0%
Chondracar	*exasperatus*	0%	0%	0%	0%	0%	0%
Gracilaria	*cf. pacifica*	0%	0%	3%	2%	3%	6%
Mastocarpu	*papillatus*	0%	0%	0%	0%	0%	0%
Enteromorp	*intestinalis*	5%	10%	44%	22%	1%	13%
Ulva	*cf. fenestrata*	5%	2%	5%	3%	5%	6%
Anthopleura	*elegantissima*	0	0	0	0	0	0
Aequorea	*victoria*	0	0	0	0	0	0
Aurelia	*aurita*	0	0	0	0	0	0
Pleurobrach	*bachei*	0	0	0	0	0	0
Heptacarpu	*sitchensis*	0	0	0	0	0	0
Crangon	*sp.*	0	0	0	0	0	0
Pandalus	*danae*	0	0	0	0	0	0
Ligia	*pallasii*	0	0	0	0	0	0
Balanus	*glandula*	0	0	0	0	0	0
Hemigrapsu	*spp.*	0	0	2	1	0	2
Cancer	*magister*	0	0	0	0	0	0
Pagurus	*spp.*	4	0	0	0	9	3
Oregonia	*gracilis*	0	0	0	0	0	0
Pugettia	*producta*	0	0	1	0	3	0
Petrolisthes	*cinctipes*	0	0	0	0	0	0
Spiochaetop	*costarum*	6	15	7	11	17	9
Eudistylia	*vancouveri*	0	0	0	0	0	0
Alia	*carinata*	14	47	67	88	0	0
Amphissa	*versicolor*	3	0	0	1	0	2
Littorina	*spp.*	0	0	0	0	0	0
Batillaria	*zonalis*	0	0	0	0	0	0
Nucella	*lamellosa*	0	0	0	0	0	0
Archidoris	*montereyensis*	0	0	0	0	0	0
Haminoea	*virescens*	0	0	0	1	19	8
Mopalia	*muscosa*	0	0	0	0	0	0
Mytlius	*trossulus*	0	0	0	0	0	0
Lottia and *T*	*spp.*	0	0	0	0	0	0
Amphipholi	*cf. squamata*	0	0	0	0	0	0
Pisaster	*ochraceus*	0	0	0	0	0	0
Pycnopodia	*helianthoides*	0	0	0	0	0	0
Dendraster	*excentricus*	0	0	0	0	0	0
Cnemidocar	*finmarkiensis*	0	0	0	0	0	0

		Eelgrass - Site 4					
		June		July		August	
Genus	Species	Transect 1	Transect 2	Transect 1	Transect 2	Transect 1	Transect 2
Zostera	*japonica*	0%	0%	0%	0%	0%	0%
Zostera	*marina*	71%	64%	56%	39%	50%	45%
Fucus	*gardneri*	1%	0%	0%	0%	0%	0%
Leathesia	*difformis*	0%	0%	0%	0%	0%	0%
Sargassum	*muticum*	1%	0%	0%	0%	0%	0%
Calliarthron	*tuberculosum*	0%	0%	0%	0%	0%	0%
Ceramium	*californicum*	3%	3%	0%	0%	0%	0%
Chondracanthus	*exasperatus*	0%	1%	0%	0%	0%	0%
Gracilaria	*cf. pacifica*	1%	1%	4%	5%	3%	2%
Mastocarpus	*papillatus*	0%	0%	0%	0%	0%	0%
Enteromorpha	*intestinalis*	2%	4%	37%	37%	20%	10%
Ulva	*cf. fenestrata*	4%	7%	2%	4%	2%	7%
Anthopleura	*elegantissima*	0	0	0	0	0	0
Aequorea	*victoria*	0	0	0	0	0	0
Aurelia	*aurita*	0	0	0	0	0	0
Pleurobrachia	*bachei*	0	0	0	0	0	0
Heptacarpus	*sitchensis*	0	0	0	0	0	0
Crangon	sp.	0	0	0	0	0	0
Pandalus	*danae*	0	0	0	0	0	0
Ligia	*pallasii*	0	0	0	0	0	0
Balanus	*glandula*	0	0	0	0	0	0
Hemigrapsus	spp.	0	0	4	1	6	1
Cancer	*magister*	0	0	0	0	0	0
Pagurus	spp.	3	1	0	1	12	7
Oregonia	*gracilis*	0	0	0	0	0	0
Pugettia	*producta*	0	2	4	3	0	0
Petrolisthes	*cinctipes*	0	0	0	0	0	0
Spiochaetopterus	*costarum*	14	12	1	5	8	9
Eudistylia	*vancouveri*	0	0	0	0	0	0
Alia	*carinata*	27	32	44	25	113	56
Amphissa	*versicolor*	0	1	0	0	0	0
Littorina	*spp.*	0	0	0	0	0	0
Batillaria	*zonalis*	0	0	0	0	0	0
Nucella	*lamellosa*	0	0	0	0	0	0
Archidoris	*montereyensis*	0	0	0	0	0	0
Haminoea	*virescens*	10	0	0	0	0	1
Mopalia	*muscosa*	0	0	0	0	0	0
Mytlius	*trossulus*	0	0	0	0	0	0
Lottia and *Tectura*	spp.	0	0	0	0	0	0
Amphipholis	*cf. squamata*	0	0	0	0	0	0
Pisaster	*ochraceus*	0	0	0	0	0	0
Pycnopodia	*helianthoides*	0	2	0	0	0	0
Dendraster	*excentricus*	0	0	0	0	0	0
Cnemidocarpa	*finmarkiensis*	0	0	0	0	0	0

		Eelgrass - Site 5					
		June		July		August	
Genus	Species	Transect 1	Transect 2	Transect 1	Transect 2	Transect 1	Transect 2
Zostera	*japonica*	0%	0%	0%	20%	45%	4%
Zostera	*marina*	63%	68%	62%	59%	18%	56%
Fucus	*gardneri*	0%	0%	0%	0%	0%	0%
Leathesia	*difformis*	0%	0%	0%	0%	0%	0%
Sargassum	*muticum*	0%	0%	0%	0%	0%	0%
Calliarthron	*tuberculosum*	0%	0%	2%	2%	0%	0%
Ceramium	*californicum*	200%	3%	0%	0%	0%	0%
Chondracanthus	*exasperatus*	0%	0%	0%	0%	0%	0%
Gracilaria	*cf. pacifica*	0%	0%	0%	0%	0%	0%
Mastocarpus	*papillatus*	0%	0%	0%	0%	0%	0%
Enteromorpha	*intestinalis*	0%	0%	1%	0%	0%	0%
Ulva	*cf. fenestrata*	0%	0%	0%	0%	0%	0%
Anthopleura	*elegantissima*	0	0	0	0	0	0
Aequorea	*victoria*	0	0	0	0	0	0
Aurelia	*aurita*	0	0	0	0	0	0
Pleurobrachia	*bachei*	0	0	0	0	0	0
Heptacarpus	*sitchensis*	0	0	0	0	0	0
Crangon	*sp.*	0	0	0	0	0	0
Pandalus	*danae*	0	0	0	0	0	0
Ligia	*pallasii*	0	0	0	0	0	0
Balanus	*glandula*	0	0	0	0	0	0
Hemigrapsus	*spp.*	0	0	0	1	0	0
Cancer	*magister*	0	0	0	0	0	0
Pagurus	*spp.*	1	1	1	2	0	3
Oregonia	*gracilis*	0	0	0	0	0	0
Pugettia	*producta*	0	0	1	2	0	0
Petrolisthes	*cinctipes*	0	0	0	0	0	0
Spiochaetopterus	*costarum*	27	37	53	31	22	0
Eudistylia	*vancouveri*	0	0	0	1	0	0
Alia	*carinata*	0	1	18	10	1	0
Amphissa	*versicolor*	1	0	0	0	0	0
Littorina	*spp.*	0	0	0	0	0	0
Batillaria	*zonalis*	0	0	0	0	0	0
Nucella	*lamellosa*	0	0	0	0	0	0
Archidoris	*montereyensis*	0	0	0	0	0	0
Haminoea	*virescens*	0	1	0	0	5	7
Mopalia	*muscosa*	0	0	0	0	0	0
Mytlius	*trossulus*	0	0	0	0	0	0
Lottia and *Tectura*	*spp.*	0	0	0	0	0	0
Amphipholis	*cf. squamata*	0	0	0	0	0	0
Pisaster	*ochraceus*	0	0	0	0	0	0
Pycnopodia	*helianthoides*	0	0	0	0	0	0
Dendraster	*excentricus*	0	0	0	0	0	0
Cnemidocarpa	*finmarkiensis*	0	0	0	0	0	0

		Below-oyster - Site 1					
		June		July		August	
Genus	Species	Transect 1	Transect 2	Transect 1	Transect 2	Transect 1	Transect 2
Zostera	*japonica*	0%	0%	0%	0%	0%	0%
Zostera	*marina*	0%	0%	0%	0%	0%	0%
Fucus	*gardneri*	0%	0%	0%	0%	0%	0%
Leathesia	*difformis*	0%	0%	0%	0%	0%	0%
Sargassum	*muticum*	8%	8%	3%	0%	0%	0%
Calliarthron	*tuberculosum*	0%	0%	0%	0%	0%	0%
Ceramium	*californicum*	0%	0%	0%	0%	0%	0%
Chondracanthus	*exasperatus*	0%	0%	0%	0%	0%	0%
Gracilaria	cf. *pacifica*	0%	0%	0%	0%	0%	0%
Mastocarpus	*papillatus*	5%	4%	2%	2%	0%	1%
Enteromorpha	*intestinalis*	40%	83%	21%	7%	0%	0%
Ulva	cf. *fenestrata*	2%	3%	3%	1%	0%	0%
Anthopleura	*elegantissima*	0	0	0	0	0	0
Aequorea	*victoria*	0	0	0	0	0	0
Aurelia	*aurita*	0	0	0	0	0	0
Pleurobrachia	*bachei*	0	0	0	0	0	0
Heptacarpus	*sitchensis*	0	0	0	0	0	0
Crangon	sp.	0	0	0	0	0	0
Pandalus	*danae*	0	0	0	0	0	0
Ligia	*pallasii*	0	0	0	0	0	0
Balanus	*glandula*	1000	720	720	720	180	1300
Hemigrapsus	spp.	82	56	13	67	9	25
Cancer	*magister*	0	0	0	0	0	0
Pagurus	spp.	3	5	53	12	0	3
Oregonia	*gracilis*	0	0	0	0	0	0
Pugettia	*producta*	0	2	0	0	0	0
Petrolisthes	*cinctipes*	0	0	0	0	0	0
Spiochaetopterus	*costarum*	4	0	5	0	4	0
Eudistylia	*vancouveri*	0	0	0	0	0	0
Alia	*carinata*	0	0	0	0	0	0
Amphissa	*versicolor*	0	0	0	0	0	0
Littorina	spp.	0	0	0	0	0	120
Batillaria	*zonalis*	0	0	0	0	0	0
Nucella	*lamellosa*	0	0	0	0	0	0
Archidoris	*montereyensis*	0	0	0	0	0	0
Haminoea	*virescens*	0	0	0	0	0	0
Mopalia	*muscosa*	0	0	0	0	0	0
Mytlius	*trossulus*	0	0	0	0	0	2
Lottia and *Tectura*	spp.	0	0	0	240	0	80
Amphipholis	cf. *squamata*	0	0	0	0	0	0
Pisaster	*ochraceus*	0	0	0	0	0	0
Pycnopodia	*helianthoides*	0	0	0	0	0	0
Dendraster	*excentricus*	0	0	0	0	1	0
Cnemidocarpa	*finmarkiensis*	0	0	0	0	0	0

		Below-oyster - Site 2					
		June		July		August	
Genus	Species	Transect 1	Transect 2	Transect 1	Transect 2	Transect 1	Transect 2
Zostera	*japonica*	0%	0%	0%	0%	0%	0%
Zostera	*marina*	0%	0%	0%	0%	0%	0%
Fucus	*gardneri*	0%	0%	0%	0%	0%	0%
Leathesia	*difformis*	0%	0%	0%	0%	0%	0%
Sargassum	*muticum*	33%	27%	8%	10%	0%	0%
Calliarthron	*tuberculosum*	0%	0%	0%	0%	0%	0%
Ceramium	*californicum*	0%	1%	0%	0%	0%	0%
Chondracanthus	*exasperatus*	0%	0%	0%	0%	0%	0%
Gracilaria	cf. *pacifica*	1%	0%	1%	0%	0%	0%
Mastocarpus	*papillatus*	3%	0%	5%	5%	0%	0%
Enteromorpha	*intestinalis*	36%	32%	90%	90%	0%	2%
Ulva	cf. *fenestrata*	0%	0%	0%	0%	6%	7%
Anthopleura	*elegantissima*	0	0	0	0	0	0
Aequorea	*victoria*	0	0	0	0	0	0
Aurelia	*aurita*	0	0	0	0	0	0
Pleurobrachia	*bachei*	0	0	0	0	0	0
Heptacarpus	*sitchensis*	0	0	0	0	0	0
Crangon	sp.	0	0	0	0	0	0
Pandalus	*danae*	0	0	0	0	0	0
Ligia	*pallasii*	0	0	0	0	0	0
Balanus	*glandula*	1020	720	720	380	1300	860
Hemigrapsus	spp.	49	11	67	29	25	10
Cancer	*magister*	0	0	0	0	0	0
Pagurus	spp.	12	4	12	0	3	4
Oregonia	*gracilis*	0	0	0	0	0	0
Pugettia	*producta*	0	1	0	0	0	0
Petrolisthes	*cinctipes*	0	0	0	0	0	0
Spiochaetopterus	*costarum*	0	0	0	0	0	4
Eudistylia	*vancouveri*	0	0	0	0	0	0
Alia	*carinata*	0	0	0	0	0	0
Amphissa	*versicolor*	0	0	0	0	0	0
Littorina	*spp.*	0	0	0	0	120	0
Batillaria	*zonalis*	0	0	0	0	0	0
Nucella	*lamellosa*	5	8	0	6	0	3
Archidoris	*montereyensis*	1	0	0	0	0	0
Haminoea	*virescens*	0	0	0	0	0	0
Mopalia	*muscosa*	0	0	0	0	0	0
Mytlius	*trossulus*	0	0	0	0	2	0
Lottia and *Tectura*	spp.	67	0	240	0	80	49
Amphipholis	cf. *squamata*	0	0	0	0	0	0
Pisaster	*ochraceus*	0	0	0	0	0	0
Pycnopodia	*helianthoides*	0	0	0	0	0	0
Dendraster	*excentricus*	0	0	0	0	0	0
Cnemidocarpa	*finmarkiensis*	0	1	0	0	0	0

		Below-oyster - Site 3					
		June		July		August	
Genus	Species	Transect 1	Transect 2	Transect 1	Transect 2	Transect 1	Transect 2
Zostera	*japonica*	0%	0%	0%	0%	0%	0%
Zostera	*marina*	0%	0%	0%	0%	0%	0%
Fucus	*gardneri*	0%	0%	0%	0%	0%	0%
Leathesia	*difformis*	0%	0%	0%	0%	0%	0%
Sargassum	*muticum*	10%	11%	0%	3%	1%	0%
Calliarthron	*tuberculosum*	0%	0%	0%	0%	0%	0%
Ceramium	*californicum*	0%	4%	0%	0%	0%	0%
Chondracanthus	*exasperatus*	0%	0%	0%	0%	0%	0%
Gracilaria	*cf. pacifica*	0%	0%	0%	0%	0%	0%
Mastocarpus	*papillatus*	4%	3%	3%	4%	6%	4%
Enteromorpha	*intestinalis*	15%	48%	71%	65%	4%	10%
Ulva	*cf. fenestrata*	0%	0%	2%	1%	160%	280%
Anthopleura	*elegantissima*	0	0	0	0	0	0
Aequorea	*victoria*	0	0	0	0	0	0
Aurelia	*aurita*	0	0	0	0	0	0
Pleurobrachia	*bachei*	0	0	0	0	0	0
Heptacarpus	*sitchensis*	0	0	0	0	0	0
Crangon	sp.	0	0	0	0	0	0
Pandalus	*danae*	0	0	0	0	0	0
Ligia	*pallasii*	0	0	0	0	0	0
Balanus	*glandula*	580	860	440	880	580	300
Hemigrapsus	spp.	1	1	6	1	4	7
Cancer	*magister*	0	0	0	0	0	0
Pagurus	spp.	1	0	5	11	4	5
Oregonia	*gracilis*	0	0	0	0	0	0
Pugettia	*producta*	0	0	0	0	0	1
Petrolisthes	*cinctipes*	0	0	1	1	0	0
Spiochaetopterus	*costarum*	0	1	0	0	0	0
Eudistylia	*vancouveri*	0	0	0	0	0	0
Alia	*carinata*	0	0	10	10	0	21
Amphissa	*versicolor*	0	0	1	2	0	0
Littorina	*spp.*	0	0	0	0	0	0
Batillaria	*zonalis*	0	0	0	0	0	0
Nucella	*lamellosa*	0	0	0	0	0	0
Archidoris	*montereyensis*	0	0	0	0	0	0
Haminoea	*virescens*	0	0	1	0	0	0
Mopalia	*muscosa*	0	0	0	0	0	0
Mytlius	*trossulus*	0	0	0	0	0	0
Lottia and *Tectura*	spp.	0	0	0	1	0	0
Amphipholis	*cf. squamata*	0	0	0	3	0	0
Pisaster	*ochraceus*	0	0	1	0	0	0
Pycnopodia	*helianthoides*	0	0	0	0	0	0
Dendraster	*excentricus*	0	0	0	0	0	0
Cnemidocarpa	*finmarkiensis*	0	0	0	0	0	0

		Below-oyster - Site 4					
		June		July		August	
Genus	Species	Transect 1	Transect 2	Transect 1	Transect 2	Transect 1	Transect 2
Zostera	*japonica*	0%	0%	0%	0%	0%	0%
Zostera	*marina*	0%	1%	0%	0%	0%	0%
Fucus	*gardneri*	0%	0%	0%	0%	4%	0%
Leathesia	*difformis*	0%	0%	0%	0%	0%	0%
Sargassum	*muticum*	58%	80%	14%	11%	0%	0%
Calliarthron	*tuberculosum*	0%	0%	0%	0%	0%	0%
Ceramium	*californicum*	3%	3%	1%	0%	0%	0%
Chondracanthus	*exasperatus*	0%	0%	0%	0%	0%	0%
Gracilaria	cf. *pacifica*	1%	0%	0%	0%	0%	0%
Mastocarpus	*papillatus*	1%	1%	3%	3%	2%	1%
Enteromorpha	*intestinalis*	0%	0%	87%	80%	12%	9%
Ulva	cf. *fenestrata*	0%	0%	0%	0%	3%	4%
Anthopleura	*elegantissima*	0	0	0	1	0	0
Aequorea	*victoria*	0	0	0	0	0	0
Aurelia	*aurita*	0	0	0	0	0	0
Pleurobrachia	*bachei*	0	0	0	0	0	0
Heptacarpus	*sitchensis*	0	0	0	0	0	0
Crangon	sp.	0	0	0	0	0	0
Pandalus	*danae*	0	0	0	0	0	0
Ligia	*pallasii*	0	0	0	0	0	0
Balanus	*glandula*	440	720	300	440	1600	1460
Hemigrapsus	spp.	0	0	4	3	20	41
Cancer	*magister*	0	0	0	0	0	0
Pagurus	spp.	1	1	5	0	7	7
Oregonia	*gracilis*	0	0	0	0	0	0
Pugettia	*producta*	0	1	0	1	0	0
Petrolisthes	*cinctipes*	0	0	0	0	4	0
Spiochaetopterus	*costarum*	0	2	0	0	0	5
Eudistylia	*vancouveri*	0	0	0	0	0	0
Alia	*carinata*	0	0	6	1	12	4
Amphissa	*versicolor*	0	0	1	0	0	0
Littorina	*spp.*	0	0	0	0	0	0
Batillaria	*zonalis*	0	0	8	12	0	0
Nucella	*lamellosa*	0	0	0	0	1	0
Archidoris	*montereyensis*	0	0	0	0	0	0
Haminoea	*virescens*	0	0	0	0	0	0
Mopalia	*muscosa*	0	0	0	0	1	0
Mytlius	*trossulus*	0	0	0	0	0	0
Lottia and *Tectura*	spp.	0	0	0	0	17	10
Amphipholis	cf. *squamata*	0	0	0	0	2	1
Pisaster	*ochraceus*	4	0	1	2	0	0
Pycnopodia	*helianthoides*	0	0	0	0	0	0
Dendraster	*excentricus*	0	0	0	0	0	0
Cnemidocarpa	*finmarkiensis*	0	0	0	0	0	0

		Eelgrass seines			Below-oyster seines		
Genus	Species	Site E1	Site E5	Site E7	Site BO2	Site BO4	Site BO5
Anthopleura	*elegantissima*	0	0	0	0	0	0
Aequorea	*victoria*	160	32	20	0	25	34
Aurelia	*aurita*	2	0	0	0	1	0
Pleurobrachia	*bachei*	17	0	20	1	22	19
Heptacarpus	*sitchensis*	7	20	0	0	0	0
Crangon	sp.	20	19	10	0	0	0
Pandalus	*danae*	24	32	1	0	0	0
Ligia	*pallasii*	5	0	0	0	1	0
Balanus	*glandula*	0	0	0	0	0	0
Hemigrapsus	spp.	1	1	0	1	1	0
Cancer	*magister*	2	3	1	0	0	0
Pagurus	spp.	2	2	0	0	3	0
Oregonia	*gracilis*	3	0	0	0	0	0
Pugettia	*producta*	32	57	4	2	0	0
Petrolisthes	*cinctipes*	0	0	0	0	0	0
Spiochaetopterus	*costarum*	0	0	0	0	0	0
Eudistylia	*vancouveri*	0	0	0	0	0	0
Alia	*carinata*	0	17	0	0	0	0
Amphissa	*versicolor*	0	0	0	0	0	0
Littorina	*spp.*	0	0	0	0	0	0
Batillaria	*zonalis*	0	0	0	0	0	0
Nucella	*lamellosa*	0	0	0	0	0	0
Archidoris	*montereyensis*	0	0	0	0	0	0
Haminoea	*virescens*	18	455	52	0	0	0
Mopalia	*muscosa*	0	0	0	0	0	0
Mytlius	*trossulus*	0	0	0	0	0	0
Lottia and *Tectura*	spp.	0	0	0	0	0	0
Amphipholis	cf. *squamata*	0	0	0	0	0	0
Pisaster	*ochraceus*	0	0	0	0	0	0
Pycnopodia	*helianthoides*	0	0	0	0	0	0
Dendraster	*excentricus*	0	0	0	0	0	0
Cnemidocarpa	*finmarkiensis*	0	0	0	0	0	0

		Eelgrass seines			Below-oyster seines		
Genus	Species	Site E1	Site E5	Site E7	Site BO2	Site BO4	Site BO5
Leptocottu	*armatus*	161	21	73	10	12	3
Cottus	*asper*	3	0	0	0	0	0
Clinocottus	*globiceps*	1	0	0	0	0	0
Oligocottu	*maculosus*	0	1	0	0	0	0
Artedius	*fenestralis*	0	1	1	0	0	0
Psychrolut	*paradoxus*	0	1	2	0	0	0
Psettichthy	*melanostic*	1	10	3	0	0	0
Pleuronich	*coenosus*	1	0	0	0	0	0
Platichthys	*stellatus*	19	0	17	0	0	0
Citharichth	*sordidus*	1	20	1	0	0	0
Apodichth	*flavidus*	2	0	1	0	0	0
Xererpes	*fucorum*	3	3	0	0	1	0
Pholis	*laeta*	2	4	0	0	0	0
Pholis	*ornata*	0	34	18	0	0	0
Rhacochil	*vacca*	17	0	0	0	5	0
Cymatoga	*aggregata*	0	68	110	0	0	0
Syngnathu	*griseolinea*	52	50	10	0	2	0
Porichthys	*notatus*	185	20	0	0	0	0
Ammodyte	*hexapterus*	29	0	0	0	0	0
Ophiodon	*elongatus*	3	0	0	0	0	0
Gasteroste	*aculeatus*	0	0	1	0	1	0
Rimicola	*muscarum*	0	1	0	0	0	0